

**FOOD AVAILABILITY, FORAGING ECOLOGY, AND ENERGETICS OF
WHOOPING CRANES WINTERING IN TEXAS**

A Dissertation

by

FELIPE CHAVEZ-RAMIREZ

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 1996

Major Subject: Wildlife and Fisheries Sciences

**FOOD AVAILABILITY, FORAGING ECOLOGY, AND ENERGETICS OF
WHOOPING CRANES WINTERING IN TEXAS**

A Dissertation

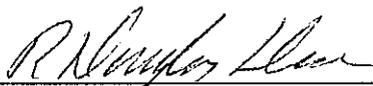
by

FELIPE CHAVEZ-RAMIREZ

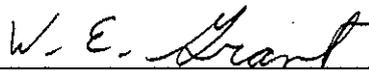
Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Approved as to style and content by:



R. Douglas Slack
(Chair of Committee)



William E. Grant
(Member)



Kirk O. Winemiller
(Member)



Merrill H. Sweet
(Member)



Robert D. Brown
(Head of Department)

May 1996

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Food Availability, Foraging Ecology, and Energetics of Whooping Cranes

Wintering in Texas. (May 1996)

Felipe Chavez-Ramirez, B.S., Sul Ross State University;

M.S., Texas A&M University

Chair of Advisory Committee: Dr. R. Douglas Slack

I investigated abundance of principal food items, foraging behavior, habitat use patterns, and winter energetics of Whooping Cranes in the salt marshes of Aransas and Matagorda Island National Wildlife Refuges on the Texas coast during the winters of 1992-93 and 1993-94. During both years of study, Whooping Cranes utilized salt marsh habitats predominantly (87% and 86%) compared to uplands (8.8% and 11%) and bays (3.9% and 3.1%). Within the salt marsh, proportional use of different mesohabitats varied among months within a winter season and between winters. Habitat use appeared to be related to availability of specific food items in each habitat. Whooping Cranes consumed primarily blue crabs, wolfberry fruit, clams, and orthopteran insects. Each major food item was consumed in a distinct mesohabitat; crabs in salt marsh open-water, wolfberries in salt marsh vegetation, clams in bays, and orthopterans in upland habitats.

Elements of foraging behavior (probing rates, progression rates) differed significantly in association with habitats and foods. Time activity budgets revealed differences in the proportion of time spent in maintenance and alert behaviors between Aransas and Matagorda Island during the first winter, and in rest and alert behavior during

the second winter. When time activity budgets were compared among different habitats during the first winter, all behaviors (feeding, locomotion, interaction, rest, maintenance, and alert) differed significantly among the four habitats of the mainland. The time spent performing certain behavioral activities differed between years for a given habitat. Food availability, disturbances, and possible predation risk associated with different locations, habitats, and years explained some of the differences in time activities.

The proportion of energetic intake contributed by different food items varied by month within and between winters. Based on energetic contribution to overall energy intake, blue crab was the most significant food item during most months of both winters. Wolfberry was the second most significant source of energy for cranes. Differential mortality between study winters and differences in reproductive success in subsequent breeding seasons suggest energy stores obtained on the wintering grounds are of great importance in determining overwinter survival and overall fitness (i.e., subsequent reproduction) of Whooping Cranes.

This dissertation is dedicated to my parents, Martina and Felipe.

They were not always sure of what I was doing or why I was out following birds, but always showed interest and support in the pursuit of my interests. They always supported and encouraged me while in graduate school and that was a very significant source of inspiration and strength during difficult times. Thanks Mom and Dad.

ACKNOWLEDGMENTS

I must thank many individuals and organizations for their support. First of all Dr. Jim Lewis, Whooping Crane Coordinator with the US Fish and Wildlife Service, for securing the funding that made this project possible. Dr. Lewis also provided input and support throughout the study. Aransas and Matagorda Island National Wildlife Refuge provided extensive logistic support for my studies. Both refuges allowed me to live and work on their premises with little constraints. Brent Giezentanner and Chris Pease were instrumental in the support that I received from the entire staff of the two refuges. The staff of both refuges were always helpful I thank them all. I want to especially thank Tom V. Stehn, Refuge Biologist at Aransas, for the informative discussions and assistance that he provided during the entire period that I was on Aransas. Texas Parks and Wildlife Department, Rockport office, provided the crab traps for my study.

My advisor, R. Doug Slack, provided extensive support and helpful discussions on different aspects of my field work and during the writing of this dissertation. I will always be grateful to Doug for the confidence that he showed in my ability and the opportunity to conduct this research. I want to thank the rest of my committee members, Drs. Kirk O. Winemiller, William E. Grant, and Merrill H. Sweet, for comments and advice throughout this project.

My family and friends deserve a special note of gratitude, because though not directly involved with my project their support and confidence always makes difficult and

stressful situations easier to deal with. I want to highlight the interactions and support that came about through the overlap in my study with that of Jerrad Van't Hull. His presence on Matagorda Island, and the friendship that developed between us, made the field experience a much more enjoyable one.

I want to especially thank my wife, Gennie. She has continued to provide support and encouragement through all my years in graduate school, sometimes at the expense of her own career. It is hard to imagine what it would have been like during the time I was conducting research and taking classes if she had not been around.

One's professional career is always influenced directly and indirectly by the interactions with many people. I can think of several individuals, professors and colleagues, with whom I interacted that greatly enhanced my professional development and peaked my interests while at Texas A&M University. While I can not define specifically what each individual's influence was here, I want to recognize the following individuals: Doug Slack, Dale Gawlik, Jane Packard, Milton Weller, Bill Grant, Nova Silvy, Kirk Winemiller, Ken Risenhoover, Dean Ransom, and the many graduate students with whom I had entertaining and productive discussions.

TABLE OF CONTENTS

	PAGE
ABSTRACT.....	iii
DEDICATION.....	v
ACKNOWLEDGMENTS.....	vi
TABLE OF CONTENTS.....	viii
LIST OF FIGURES.....	xi
LIST OF TABLES.....	xii
 CHAPTER	
I INTRODUCTION.....	1
Diet and foraging behavior.....	2
Habitat use.....	3
Theoretical framework.....	4
Objectives.....	6
 II HABITAT USE PATTERNS, FORAGING BEHAVIOR, AND	
SOCIALITY OF NON-BREEDING WHOOPING CRANES.....	8
Synopsis.....	8
Introduction.....	9
Methods.....	12
Study area.....	12
Food availability.....	13
Habitat use.....	14
Social interactions.....	15
Winter movements.....	16
Foraging behavior.....	16
Statistical analysis.....	17
Results.....	18
Food availability.....	18
Habitat use.....	21

TABLE OF CONTENTS (continued)

CHAPTER	PAGE
Winter movements and sociality.....	28
Foraging behavior.....	29
Discussion.....	34
Habitat use, food use, and foraging behavior.....	34
Movements and sociality.....	39
III SPATIAL AND INTERSEASONAL EFFECTS ON TIME ACTIVITY	
BUDGETS OF WINTERING WHOOPING CRANES.....	42
Synopsis.....	42
Introduction.....	43
Methods.....	46
Results.....	48
Discussion.....	54
Spatial effects.....	54
Among habitat effects.....	56
Between year effects.....	59
IV TEMPORAL PATTERNS IN ENERGETIC BUDGETS	
OF WINTERING WHOOPING CRANES.....	62
Synopsis.....	62
Introduction.....	63
Methods.....	67
Daily energy expenditure.....	69
Energy consumption.....	73
Energy balance model assumptions.....	76
Results.....	77
Monthly energy budgets.....	77
Energetic contribution of food items.....	77
Discussion.....	81
Overwinter survival and reproductive success.....	82
Population energetics.....	86

TABLE OF CONTENTS (continued)

CHAPTER	PAGE
V SUMMARY AND CONCLUSIONS.....	87
LITERATURE CITED.....	92
VITA.....	104

LIST OF FIGURES

FIGURE		PAGE
1	Phenology and abundance of wolfberry fruit in salt marsh areas of Aransas and Matagorda Island National Wildlife Refuges during 1992-93 winter.....	19
2	Blue crab trapping success in open water areas of the salt marsh in Aransas and Matagorda Island National Wildlife Refuges during winters of 1992-93 and 1993-94. Week 1 is first week in October.....	20
3	Proportion of Whooping Crane wintering population observed in salt marsh vegetation habitat in Aransas and Matagorda Island National Wildlife Refuges during 1992-93 overwintering season.....	22
4	Proportion of Whooping Crane population observed in different open water habitats of the salt marsh in Aransas and Matagorda Island National Wildlife Refuges during the 1992-93 overwintering season....	23
5	Proportion of Whooping Crane population observed in bay and upland habitats of Aransas and Matagorda Island National Wildlife Refuges during the 1992-93 overwintering season.....	24

LIST OF TABLES

TABLE		PAGE
1	Numbers of Whooping Cranes observed in different habitats during different months of 1992-93 winter on the Texas coast.....	26
2	Numbers of Whooping Cranes observed in different habitats during different months of 1993-94 winter on the Texas coast.....	27
3	Number, size, and, social classification of Whooping Crane groups located in salt marsh and upland habitats on the Texas coast from 1992-94.....	30
4	Foraging attributes of wintering Whooping Cranes in different habitats and years on the Texas coast. Numbers are means and standard deviations (SD).....	31
5	Type and quantity of prey items consumed by Whooping Cranes while in different habitats of the salt marsh on the Texas wintering grounds during two winters.....	33
6	Time activity budgets of Whooping Cranes during winters of 1992-93 and 1993-94 on Aransas and Matagorda Island National Wildlife Refuges.....	50
7	Time activity budgets of Whooping Cranes during the 1992-93 winter in different habitats of Aransas and Matagorda Island National Wildlife Refuges on the Texas coast.....	51
8	Time activity budgets of Whooping Cranes during the 1993-94 winter in different habitats of Aransas and Matagorda Island National Wildlife Refuges on the Texas coast.....	52

LIST OF TABLES (continued)

TABLE		PAGE
9	Behavior categories used in this study and energy expenditure coefficients (EEC) used to estimate daily energy expenditure (DEE) of Whooping Cranes wintering on the Texas coast.....	70
10	Gross energy content and metabolizable energy coefficients for Whooping Crane foods from Texas wintering grounds on dry matter basis.....	74
11	Daily energy expenditure (DEE), daily energy intake (DEI), and daily energetic balance of Whooping Cranes wintering on the Texas coast.....	79
12	Total net and proportion of daily energy obtained from different food items during different months by Whooping Cranes wintering on the Texas coast.....	80

CHAPTER I

INTRODUCTION

The Aransas-Wood Buffalo National Park Whooping Crane (Grus americana) population is the sole remaining, self-sustaining wild flock of this endangered species. The population of Whooping Cranes breeds in Woods Buffalo National Park in Canada and winters from mid-October through mid-April at the Aransas National Wildlife Refuge (ANWR) and surrounding areas of Texas coastal marsh. The Aransas population of Whooping Cranes has gradually increased from a low of 16 individuals in 1941 to a high of 146 birds during the 1989-90 and 1990-91 winter. The population numbered 132 birds during the winters of 1991-92, 136 during 1992-93 and 143 individuals during the 1993-94 winter.

As the Whooping Crane population has increased so has the area of occupied winter habitat. The increase in winter habitat range, however, has not been in proportion to population increases. New pairs tend to establish territories near their parents causing a declining trend in average territory size (Stehn and Johnson 1987). As more cranes occupy the winter habitat, and territory area is reduced in size, the possibility exists for a decline in the food base for individual pairs of territorial Whooping Cranes.

DIET AND FORAGING BEHAVIOR

The diet of wintering Whooping Cranes has been assessed through visual observation, examination of fecal pellets, analysis of digestive tracts of dead birds, and the evaluation of potential food items from known organisms in the marsh. Early work on Whooping Crane diets was largely anecdotal and much of the food items reportedly eaten by the cranes were based on assumptions and supported by scant data (Nuttall 1834, Audubon 1841, Goss 1886). Early observations of Whooping Crane foods were summarized by Bent (1926) and Netting (1927).

Since the establishment of the ANWR in 1937, several individuals have made observations of Whooping Crane feeding and of food items consumed on the wintering grounds. Stevenson and Griffith (1946) published qualitative observations of and results of a study of fecal droppings. All information gathered before 1951 is summarized in Allen (1952). Since Allen's (1952) publication, other studies have continued to document the diet of Whooping Cranes at ANWR. Uhler and Locke (1969) looked at stomach contents of one Whooping Crane, while Blankinship (1976) reportedly used direct observation and study of fecal samples. Hunt and Slack (1987) examined the contents of two crane esophaguses and gizzards and reported on the results of fecal samples collected at Aransas (Hunt and Slack 1989). The primary food items identified in previous studies of wintering Aransas birds include blue crabs (Callinectes sapidus), razor clams (Tagellus plebius), wolfberry (Lycium carolinianum), fiddler crabs (Uca spp.), plicate horn shells (Cerithidae pliculosa), other snails (Melampus coffeus), (Cyperus spp.), (Littorina spp.), shrimp (Panaeus spp.), crayfish (Cambarus hedgpethi), and acorns (Quercus virginiana). Less

commonly fish, snakes, and insects are also taken by Whooping Cranes on the Texas coast. While food items in the diet of Whooping Cranes are well known, little is known regarding the availability of different food items, Whooping Crane prey preferences, foraging strategies, and food resource use on the wintering grounds.

Temporal patterns of food and habitat use by wintering Whooping Cranes have been reported. In studies conducted over several months, changes have been noted in primary feeding locations (Blankinship 1976, Bishop 1984) and food items taken throughout the winter period (Blankinship 1976, Hunt and Slack 1989). Groups of cranes observed in the uplands are reported to be responding to increased availability of acorns (Bishop 1984, Hunt 1987, Stehn pers. comm.) and corn (Stevenson and Griffith 1946, Shields and Benham 1969). Aggregations of cranes have also been observed in the marshes (Bishop 1984). Explanations are given for the observed concentrations but they are based on qualitative assumptions and little, in some cases no, quantitative data exist.

HABITAT USE

Habitat use by Whooping Cranes wintering on the Texas coast has only been studied at large spatial scales (i.e. marsh, upland, etc.). The primary habitat used by cranes at a large scale is the salt marsh or salt flats (Stevenson and Griffith 1946, Allen 1952, Labuda and Butts 1978), although use of bay and uplands has also been reported (Bishop 1984, Hunt 1987). The salt marsh is actually a heterogenous habitat composed of a variety of microhabitats at smaller scales. Stevenson and Griffith (1946) recognized brackish ponds, tidal lagoons or sloughs, shallow bays, and inlet ponds within salt marshes. Allen

(1952) recognized several open water categories: permanent, semipermanent, and ephemeral ponds and lakes. The biotic and abiotic factors affecting differential use of salt marsh meso- and microhabitats by Whooping Cranes have not been determined.

Whooping Crane use of upland areas has been described previously (Allen 1952, Bishop and Blankinship 1982, Bishop 1984, Hunt 1987) and is reported to be in response to availability of acorns (Allen 1952, Bishop 1984, Hunt 1987), wolfberry (Hunt 1987), paspalum grasses (Stevenson and Griffith 1946), and cultivated crops (Shields and Benham 1969). Acorns are considered such an important food item for Whooping Cranes that ANWR refuge conducts several prescribed burns of uplands each winter to improve the crane's access to acorns. A recent evaluation of Whooping Crane use of upland habitats suggests that Whooping Cranes utilize recently burned areas regardless of acorn availability (Chavez-Ramirez et al. 1996). Use of shallow bay areas by Whooping Cranes appears to be related to feeding on clams (Blankinship 1976, T. Stehn pers. comm.). A study that estimates the distribution and abundance of the primary food items in different microhabitats and their relation to food use, patterns of habitat use, and energetics of Whooping Cranes wintering in Texas is needed to further conservation efforts and improve management for this endangered species.

THEORETICAL FRAMEWORK

Resource use is influenced by constraints associated with species morphology, physiology, and behavior plus external factors such as availability of alternative food types, spatial relationships among resource attributes, attributes of the resources themselves, or

competition with other species (Wiens 1989). During the nonbreeding season, food is the resource of primary importance, and the acquisition of food should play a prominent role in determining a bird's use of space and time (Hutto 1985). Birds should spend most of their foraging time in areas that yield the highest food intake rates.

Microhabitat use by birds can vary over time and changes in patterns should be most apparent when resource levels change markedly (Wiens 1989). Differences in individual foraging behavior between specific habitats suggest differential quality of resources or variations in resource availability (MacArthur 1958, 1972, Kushlan 1976, Wiens 1989). Diets of species change as prey abundance and availability vary in both space and time (Schluter 1982), which may be reflected in changes in patterns of habitat use (Ulfstrand 1976, Hejl and Verner 1990, Miles 1990, Lundquist and Manuwal 1990) and/or foraging behavior (Holmes 1966, Sealy 1979, Alatalo 1980, Morrison and With 1987, Hejl and Verner 1990, Ford et al. 1990). Observed patterns of habitat use should reflect, to some extent, Whooping Crane food use. Habitat use patterns together with knowledge of the seasonal abundance and potential availability of food resources in different habitats should allow for the evaluation of whether or not Whooping Cranes are selecting habitats based on food abundance, food availability, or prey preference.

A complete assessment of foraging ecology must consider nutritional and energetic relationships in addition to the behavioral attributes of the animal under study (Morrison et al. 1992). No energetic studies have been conducted on the Whooping Crane or its food resources on the wintering grounds. The study of time and energy budgets is a convenient way to evaluate effects of changing foraging behaviors and prey availability on an animal's

energy balance (Goldstein 1990, Pianka 1994). An understanding of the energy costs of different activities provides a means for evaluating the costs and benefits of changing activity budgets due to changes in foraging and behavioral strategies (Goldstein 1990).

In the nonbreeding season, food availability should be the major factor influencing a bird's time budget (Hutto 1985, Martin 1986). With shorter days and usually less predictable food supply, winter is the period of energy "crunch" for temperate zone birds (Weathers and Sullivan 1993), making it a challenging time for balancing energy budgets. Behavioral changes as well as other factors (habitat location, prey) may be selected to reduce energy costs of foraging (Pienkowski et al. 1984). Habitat switching or changing feeding behaviors in response to changes in patterns of prey availability (Kushlan 1976) alter activity budgets of birds. Within the same habitat, we expect changes in food availability to be reflected by the time spent performing different activities (such as feeding and locomotion). In addition to the biological factors influencing a bird's foraging behavior and activity budgets, abiotic environmental factors may strongly affect foraging and time budgets (Goldstein 1990, Morse 1990, Morrison et al. 1992).

OBJECTIVES

The overall objective of this research was to determine how the distribution and abundance of food resources are related to Whooping Crane habitat use patterns, foraging ecology, and winter energetic balance. Specific objectives included:

- A) Estimation of the distribution and abundance of the principal food items of Whooping Cranes in salt marsh microhabitats.

- B) Determination of macro- and mesohabitat use patterns in relation to availability of food resources.
- C) Evaluation of foraging differences and behavioral activity budgets in relation to food type and habitats.
- D) Development of an energetic model based on time activity budgets to evaluate effects of changes in food availability on the daily energy balance of cranes.

CHAPTER II

HABITAT USE PATTERNS, FORAGING BEHAVIOR, AND SOCIALITY OF NON-BREEDING WHOOPING CRANES

SYNOPSIS

I studied habitat use and foraging ecology of wintering Whooping Cranes on the Texas coast. I report on temporal patterns of macro- and mesoscale habitat use by Whooping Cranes in relation to seasonal patterns of food availability. Foraging behavior and prey consumption rates were quantified and compared among mesohabitats. I also evaluated the potential effect of reduced prey availability on crane movements and social interactions between macrohabitats and years. Availability of primary food items (wolfberry, blue crab, clams) changed seasonally and yearly during the study period. Based on aerial surveys conducted over the two winters of study, Whooping Cranes utilized salt marsh macrohabitats predominantly (87% and 86%) compared to upland (8.8% and 11%) and bay habitats (3.9% and 3.1%). Proportional use of specific mesohabitats within the salt marsh varied among months during a winter season and between winters, and appeared to be related to availability of specific food items in each habitat. The mean proportion of the wintering crane population detected per aerial survey was significantly different between years (96.7% first year and 89.4% second year) suggesting cranes may have moved away from their normal activity range in the salt marsh during the second season. Size of Whooping Crane social groups and those that included cranes other than family members differed among habitats ($\chi^2 = 20.3$ $P < 0.05$). In salt marsh habitats 19.2% and 13% of

groups involved non-family members during 1992-93 and 1993-94 winters respectively, while in upland habitats 54.3% and 75% involved non-family groups. Probing (probes/min) and progression rates (steps/min) of cranes showed differences among different habitats. During the winter of 1992-93, differences ($P = 0.001$) were observed between progression rates but not probing rate ($P = 0.46$). Likewise during the 1993-94 winter significant differences were found in progression rates ($P = 0.01$) but not probing rates ($P = 0.41$) among habitats. The estimated number of wolfberries consumed per hr increased approximately 30% from first to second winter of study, while numbers of blue crabs consumed per hr decreased by more than 50% (7.1 vs 2.8).

INTRODUCTION

The use of food resources in birds is influenced by constraints associated with the morphology, physiology, and behavior of the species. The use of resources is also influenced by external factors such as availability of alternative food types, spatial relationship among resource attributes, attributes of the resources themselves, or competition with other species (Wiens 1989). In temperate species the nonbreeding season is a period during which food is the resource of primary importance, and the acquisition of food should play a prominent role in determining a bird's use of space and time (Hutto 1985).

Use of microhabitats can vary over time, and changes in patterns should be most apparent when resource levels change substantially (Wiens 1989). Differences in individual foraging behavior among different habitats suggest differential use of resources or differences in resource availability (MacArthur 1958, 1972, Kushlan 1976, Wiens 1989).

The change in a species' diet is generally the result of changes in prey abundance and availability which vary in space and time (Smith et al. 1978, Schluter 1982), and may be reflected in changes in patterns of habitat use by animals (Ulfstrand 1976, Hejl and Verner 1990, Miles 1990, Lundquist and Manuwal 1990).

The Aransas-Wood Buffalo population of Whooping Cranes (*Grus americana*) is the sole remaining, self-sustaining wild flock of this endangered species. The Aransas flock of Whooping Cranes has gradually increased from a population low of 16 individuals in 1941 to a high of 146 birds during the 1989-90 and 1990-91 winter. The population numbered 132 birds during the winter of 1991-92, 136 during 1992-93, and 143 during 1993-94. As the Whooping Crane population has increased so has the area of occupied winter habitat. The increase in winter habitat range, however, has not been in proportion to population increases. New pairs tend to establish territories near parents causing a declining trend in average territory size (Stehn and Johnson 1987). As more cranes occupy the winter habitat, and individual territory area is reduced in size, the possibility exists for a decline in the food base for pairs or family groups of territorial Whooping Cranes. A better understanding of Whooping Crane habitat use patterns and food resources availability and use is essential to advance conservation and management plans for this endangered species.

Habitat use by Whooping Cranes wintering on the Texas coast has only been studied at large geographical scales (marsh, upland, bay). The primary habitat used by cranes at a macroscale is reported to be the salt marsh or salt flats (Stevenson and Griffith 1946, Allen 1952, Labuda and Butts 1978). Other macroscale habitats, including bays and uplands, are also used by wintering Whooping Cranes (Bishop 1984, Hunt 1987). The salt marsh is a heterogenous environment composed of a variety of distinct habitats at finer scales

(mesoscale and microscale). Stevenson and Griffith (1946) were the first to recognize a subdivision at the mesoscale within the salt marsh and included brackish ponds, tidal lagoons or sloughs, shallow water bays, and inlet ponds as distinct habitats within the salt marsh. Later, Allen (1952) recognized several open water categories within the salt marsh habitat: permanent, semipermanent, and ephemeral ponds and lakes.

Specific diet items of wintering Whooping Cranes are well known. Since the establishment of the Aransas National Wildlife Refuge (ANWR) in 1937, several investigators have made observations of feeding Whooping Cranes and of specific food items consumed on the wintering grounds. Stevenson and Griffith (1946) published qualitative observations and results of a study of fecal droppings. Information gathered before 1951 is summarized in Allen (1952). Uhler and Lock (1969) looked at stomach contents of one Whooping Crane, while Hunt and Slack (1987) examined the esophagus and gizzard contents of two cranes and also reported on the results of fecal samples collected at ANWR (Hunt and Slack 1989). The primary food items identified in previous studies from wintering ANWR birds include blue crabs (Callinectes sapidus), razor clams (Tagellus plebius), wolfberry (Lycium carolinianum), fiddler crabs (Uca spp.), plicate horn shells (Cerithidae pliculosa), other snails (Melampus coffeus), (Cyperus spp.), (Littorina spp.), shrimp (Panaeus spp.), crayfish (Cambarus hedgpethi), and acorns (Quercus virginiana). Less commonly fish, snakes, and insects are also taken by Whooping Cranes on the Texas coast. While food items in the diet of Whooping Cranes are well known, little is known regarding the availability of different food items, Whooping Crane prey preferences, foraging strategies, and food resource use on the wintering grounds.

In this study I report on temporal patterns of macro- and mesoscale habitat use by

wintering Whooping Cranes in relation to seasonal patterns of availability of principal food items. Foraging behavior and prey consumption rates while feeding in different habitats and foods were examined and compared. In addition, I evaluate the potential effect of reduced prey availability on Whooping Crane movements and social interactions between and within macrohabitats.

METHODS

Study Area.-- This study was conducted on ANWR and Matagorda Island National Wildlife Refuges (MINWR) located on the Texas coast during the months of October through April of 1992-93 and 1993-94. Aransas is located in Aransas and Refugio counties and is approximately 60 km north of Corpus Christi, Texas. Matagorda Island NWR is a barrier island, 62 km long and varies from 1.2 to 7.3 km wide, located in Calhoun County. Matagorda Island runs parallel to the coastline and is east and north of ANWR. Our study of crane behavior and food sampling took place in the salt marsh portion and adjacent uplands of the two refuges, which are the primary habitats used by wintering cranes. The salt marsh area is located along the eastern coast of ANWR and on the west side of MINWR. Salt marsh habitats consist of vegetated flats dominated by glasswort (Salicornia virginiana), saltwort (Batis maritima), sea-oxeye daisy (Borrchia frutescens), wolfberry, saltgrass (Distichlis spicata), and smooth cordgrass (Spartina alterniflora). Wind tidal flats are dominated by mudflat grass (Eleocharis parvula), saltgrass, and cordgrasses. Interspersed among vegetated areas are open water bodies of varying sizes. Open water habitats within the salt marsh were classified on areal extent from smallest to largest as: pool (< 4 m²), pond (> 4 m² and < 100 m²), lake (> 100 m²). Another open water habitat

used by cranes, located adjacent to the salt marsh flats is the bay. The portion of the bay used by cranes includes the shallow open water area adjacent to the coastline up to approximately 50-80 cm deep. Upland areas adjacent to salt marsh are also used by Whooping Cranes (Chavez-Ramirez et al. 1996) and were surveyed on aerial transects. Upland habitats are dominated by scrub live oak (Quercus virginiana), and grasslands dominated by marshhay cordgrass (Spartina patens). Two sampling sites were located on each refuge to evaluate food distribution and abundance, and as primary sites to conduct observations of crane foraging behavior and food use.

Food Availability.-- To determine the distribution and abundance of blue crabs, crab traps were baited and set in open water habitats of the salt marsh between October 1992 and April 1994. Crab traps were set every two weeks, during alternating weeks on each refuge from October through April and monthly from May through September. Traps were baited early morning one day and were checked for crabs 24 hrs later. Bait was removed from traps and traps were set outside of water until the next trapping session. Crab abundance is reported as mean number of crabs per trap during each sampling period.

Wolfberry abundance was evaluated at each of the two sampling areas approximately every two weeks on each refuge. Thirty - 1 m² quadrats were located at each site running perpendicular to the coastline, between bay edge and the upland edge of the salt marsh. Both ripe and green wolfberry fruits were counted and recorded on each quadrat. Wolfberry abundance during each survey is reported as number of berries per 30 m².

Sampling for clams was conducted on the shallow bay areas adjacent to the salt

marsh and in open water habitats within the marsh. A 0.25 m² benthic sampling tube and 4 mm sieve bucket were used. The tube was inserted into the sediment to a depth of 15 cm. Water was then drained from tube and the substrate was collected and sifted through the sieve bucket. Based on the Whooping Crane's bill length, a depth of 15 cm was deemed the depth at which Whooping Cranes could probe into the sediment and capture prey.

Sampling for snails was attempted by randomly placing a 0.5 m² quadrat and then searching intensively through the vegetation and substrate within the plot for snails. Because snails were relatively rare and were patchily distributed throughout the salt marsh, measurement of snail abundance occurred in quadrats placed in regions of the salt marsh where snails and/or shells had been previously located.

Habitat Use.-- Habitat use was evaluated almost weekly during 1992-93 by locating as many individual cranes as possible on the winter range as part of ANWR census flights from a fixed-wing aircraft. During 1993-94 only eight surveys were completed due to logistical difficulties, which included mechanical problems with the aircraft and bad weather. The specific habitat where each crane was standing at the time of initial observation was recorded. Use of initial observation is preferred for estimating common foraging locations of birds (Hejl et al. 1990). A single record was taken of each individual observed during each survey so as to maintain independence between data points (Morrison et al. 1992). Habitat use by Whooping Cranes was evaluated at two different scales, macro- and mesoscales. At the macroscale, three habitats were recognized and included coastal salt marsh, uplands, and bays. Mesohabitats recognized within the salt marsh included salt marsh vegetation, salt marsh open water (pools, ponds, and lakes as classified above), and

flats (sand and mud). Other mesohabitats recognized within uplands included, grasslands, burned areas, and freshwater ponds. Monthly habitat use patterns were compared using survey data for the 1992-93 season pooled by month, except February and March which were combined because only two surveys were conducted each month. During 1993-94, surveys were pooled for the months of December and January only, because of the limited number of surveys completed during all other months during that winter.

Social Interactions.-- For each crane recorded on aerial surveys, the number of associates or group size (other Whooping Cranes) was recorded. During each season, the number of social groups (2 or more cranes), mean group size, and maximum group size were estimated and compared between macrohabitats and years. Whooping Crane pairs and family groups maintain winter territories in salt marsh habitats. Mated adult Whooping Cranes stay together throughout the winter. Most adult cranes, therefore, are observed in pairs, or if nested successfully during the previous spring, in family groups of three individuals. Groups of more than three cranes are less common in salt marsh areas and, if present, are generally composed of subadults (birds in adult plumage but not mated) (Bishop 1984). Groups of Whooping Cranes, however, have been commonly observed in upland habitats (Bishop 1984, Hunt 1987, Chavez-Ramirez pers. observ.). For this study we considered an association of cranes as a non-family social group when one of two conditions was met: 1) Three individuals were present and no chicks were present, or 2) > 3 cranes present with or without chick(s) present.

Winter Movements.-- To evaluate the possibility of crane movements away from normal, or regular activity range in the wintering area, the proportion of cranes observed per survey in relation to total number of cranes known wintering in the area was calculated. The relationship between proportion of cranes observed and movement, is based on the assumption that cranes present in their normal territories (pairs and family groups) and home range (subadults) have a high probability of detection during aerial surveys because of the high visibility of cranes. Our failure to detect an individual crane during a survey was considered an indication of its absence from the normal activity range. Normal activity range is here defined as territories in case of pairs and family groups and, home range in case of subadult groups which included salt marsh and adjacent bay and upland areas. Regular Whooping Crane range at the time of this study and in recent years included ANWR, Welder Flats, Lamar Peninsula, Matagorda Island and San Jose Island.

In general, the maximum number of wintering cranes arrive on the Texas coast by early December and spring migratory activity may begin in late March. Only surveys conducted between 1 December and 18 March, of each wintering period, were used to calculate mean proportion of cranes detected per survey. During both years the same area was covered using the same flight routes with the same observers present during both years.

Foraging Behavior.-- Foraging behavioral attributes were quantified from blinds set adjacent to several Whooping Crane territories. Additional behavioral observations were conducted from towers or vehicles. During each observation session focal bird sampling (Altmann 1974) was conducted on all visible cranes. Individual cranes were sampled only once during each session to avoid possible biases due to individuals temporarily specializing

on a particular food or foraging behavior. Foraging behavior of cranes was quantified over 4 min of continuous observation, generally with the aid of 20-60X power telescope or 10X binoculars. During the 4-min observation sessions the numbers of probes and steps taken by the crane under observation were tallied using two counters. Each 4-min session was converted to a single datum as probes or steps per min and are reported as probing and progression rates, respectively. For all observations, the habitat in which the crane fed, prey type taken, and number of food items consumed were recorded. The number of food items taken by cranes per unit time was determined by counting the number of successful probes, in the case of wolfberry, and clams during the 4-min observation sessions. The number of crabs consumed per unit time was estimated by counting the number of successful crab captures over 30 consecutive min of observation. Thirty min were used because it generally took more than 4 min for a crane to find and consume each crab.

Statistical Analysis.-- Chi-square tests were used to evaluate differences in habitat use patterns among months during the 1992-93 season, differential use of habitat categories within months November - April for 1992-93, and between December and January of 1993-94. Chi-Square tests were used to evaluate differences in pattern of habitat use between winters for December and January which were the only months with at least two surveys during 1993-94 season. A Mann-Whitney U test was used to compare mean proportion of cranes observed per survey between seasons. A Chi-Square test for differences in probabilities was used to test differences in number of family and nonfamily groups between macrohabitats and within habitats between years. Differences in foraging behavior attributes within and between winters were compared among habitats with an ANOVA for

unbalanced data. T-tests were used to compare probing and progression rates between years within the same habitat.

RESULTS

Food Availability. -- Availability of food items changed seasonally and yearly. Wolfberry was abundant from fall through mid-December during both winters (Fig. 1). Blue crabs were present throughout 1992-93 but were most abundant during the first half of the sampling period (Fig. 2). During the second year, blue crabs were scarce during October and November and completely absent from traps during most of the sampling period (Fig. 2). During most of the second winter visual searches failed to detect any blue crabs until mid-January. Beginning in mid-January small crabs, too small to be retained in traps, were visually detected with numbers gradually increasing through April. Sampling for clams proved unsuccessful during the two years except for a short period of 8 - 18 March 1993. During this period dwarf clams (*Mulinia lateralis*) were abundant in the bays and were encountered in densities of 13.6 (SD = 4.4), 70.25 (SD = 9.5), and 22.8 (SD = 18.7) clams per 0.25 m² in three continuous weeks, respectively. Live clams were never obtained from open water habitats in the salt marsh. The fact that dwarf clams were collected during 1993 in bays suggests that clams may have been absent from marsh areas. Razor clams were never collected in sampling efforts. Systematic searches for live snails were completely unsuccessful. Similar negative results have been reported by others attempting to collect snails in the area (Barrera pers. comm.). Large numbers of empty plicate horn shells, however, were encountered throughout all shallow pools and some areas of marsh vegetation.

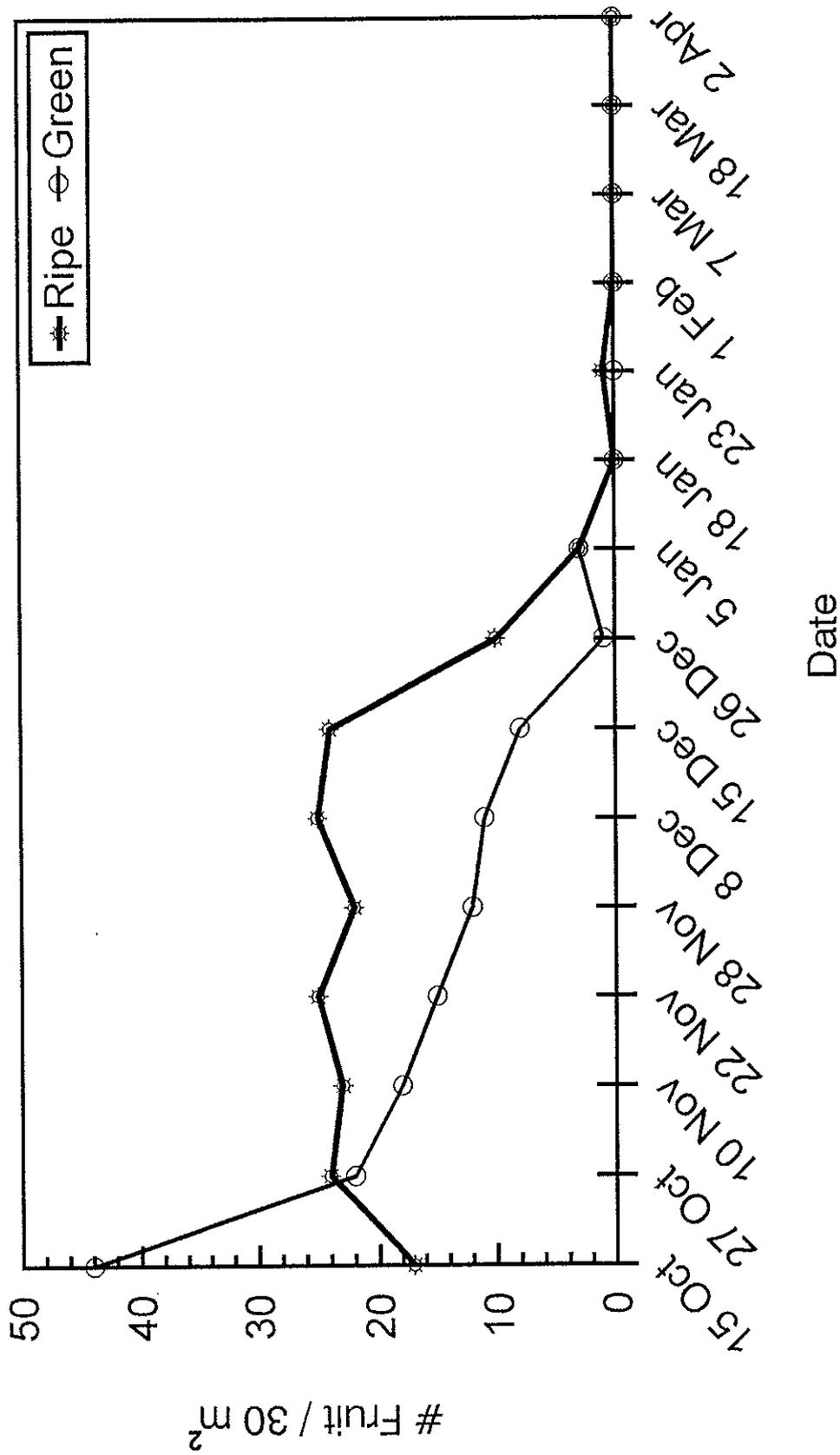


Fig. 1. Phenology and abundance of wolfberry fruit in salt marsh areas of Aransas and Matagorda Island National Wildlife Refuges during 1992-93 winter.

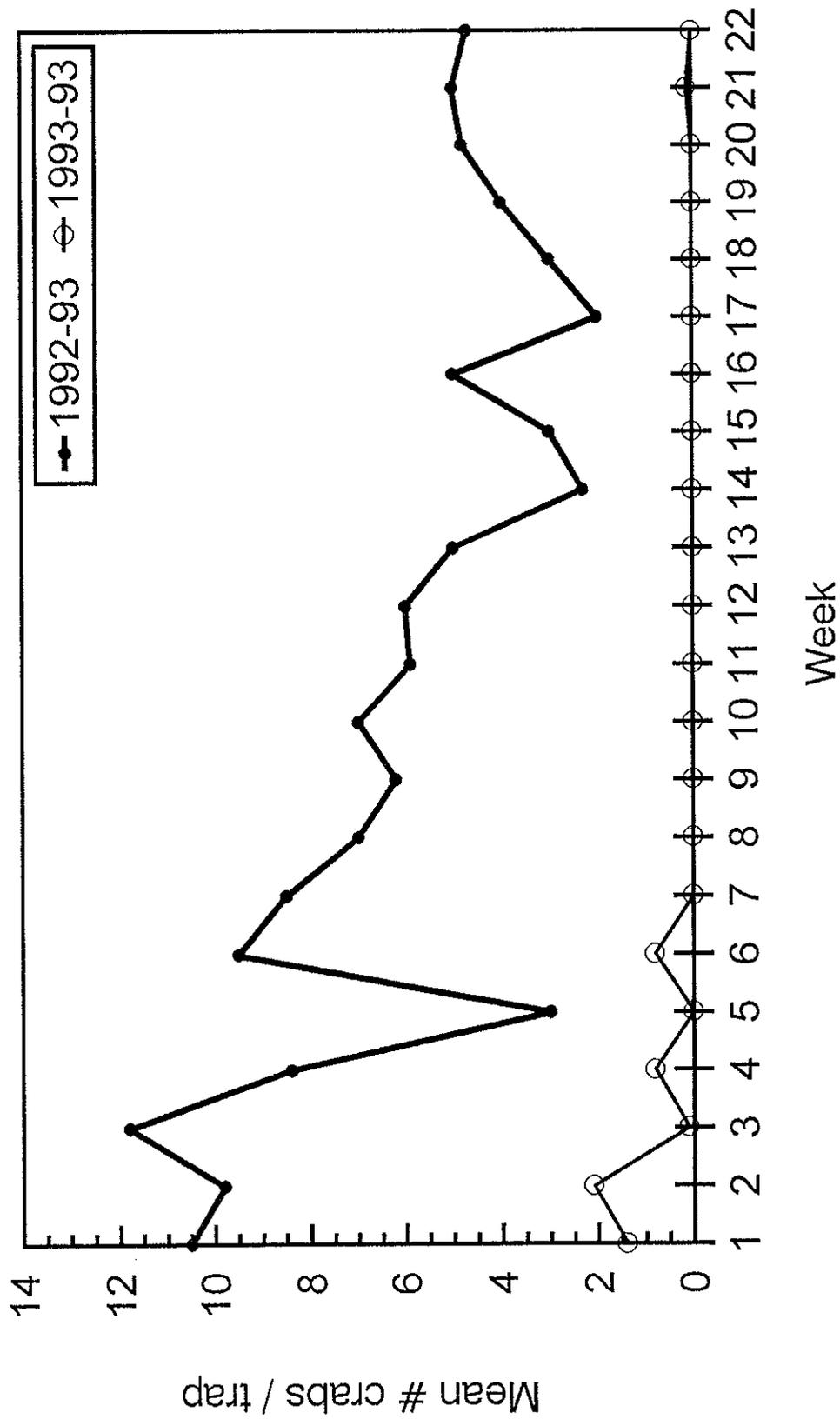


Fig. 2. Blue crab trapping success in open water areas of the salt marsh in Aransas and Matagorda Island National Wildlife Refuges during winters of 1992-93 and 1993-94. Week 1 is first week in October.

Habitat Use. -- A total of 2028 (17 surveys) and 781 (8 surveys) Whooping Crane habitat use locations were recorded on aerial surveys during the two winters, respectively. Salt marsh was the macrohabitat in which Whooping Cranes were encountered with greatest frequency during both winters. Eighty seven percent of individuals recorded on aerial surveys during the first year and 86 % of individuals during the second winter were located in salt marsh. Only 3.9 and 3.1 % of individual cranes were recorded in bays overall during 1992-93 and 1993-94, respectively. During the two winters 8.8 and 11 % of cranes were located on the upland macrohabitat.

In 1992-93 the temporal pattern of Whooping Crane use of salt marsh vegetation, based on individual surveys (Fig. 3), was generally high early in the period of overwintering and gradually declined through late February after which use of vegetated areas increased again. Overall, the pattern of use of salt marsh vegetation generally coincided with resource (wolfberry) availability (Fig. 1) in that habitat area for much of the winter. Use of specific open water habitats varied throughout the period of overwintering in 1992-93, but combined use of all open water habitats was high all winter (Fig. 4). Seasonally, the number and proportion of cranes observed per survey in bay macrohabitat was generally low during most of both wintering seasons, exceeding 10% of observations only during a single survey in April 1993 (Fig. 5). Upland habitat use was sporadic, showing low use through most of the survey period with several peaks observed at irregular intervals (Fig. 5). Each peak observed during the 1992-93 winter corresponded to a survey conducted immediately following a prescribed fire on ANWR.

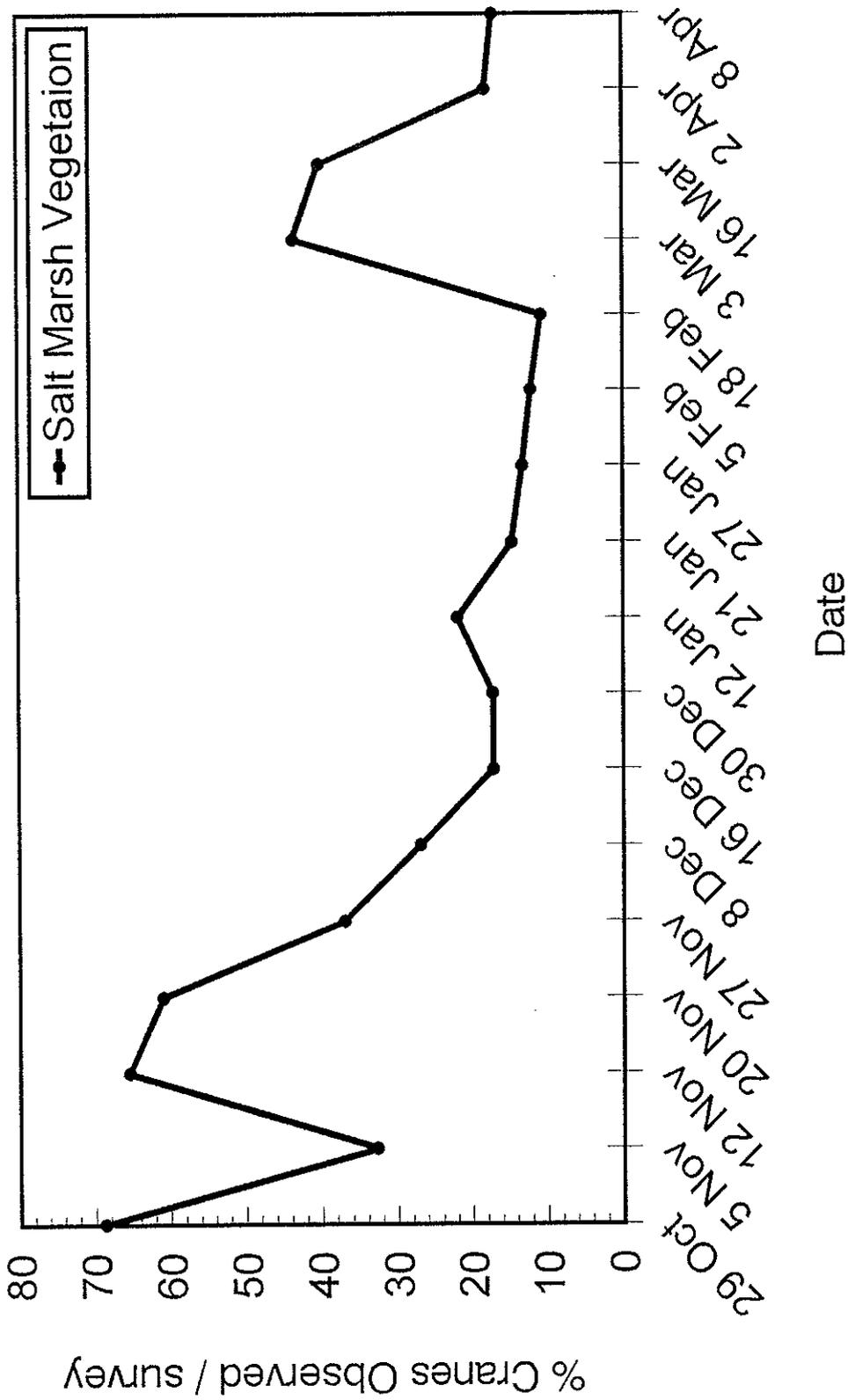


Fig. 3. Proportion of Whooping Crane wintering population observed in salt marsh vegetation habitat in Aransas and Matagorda Island National Wildlife Refuges during 1992-93 overwintering season.

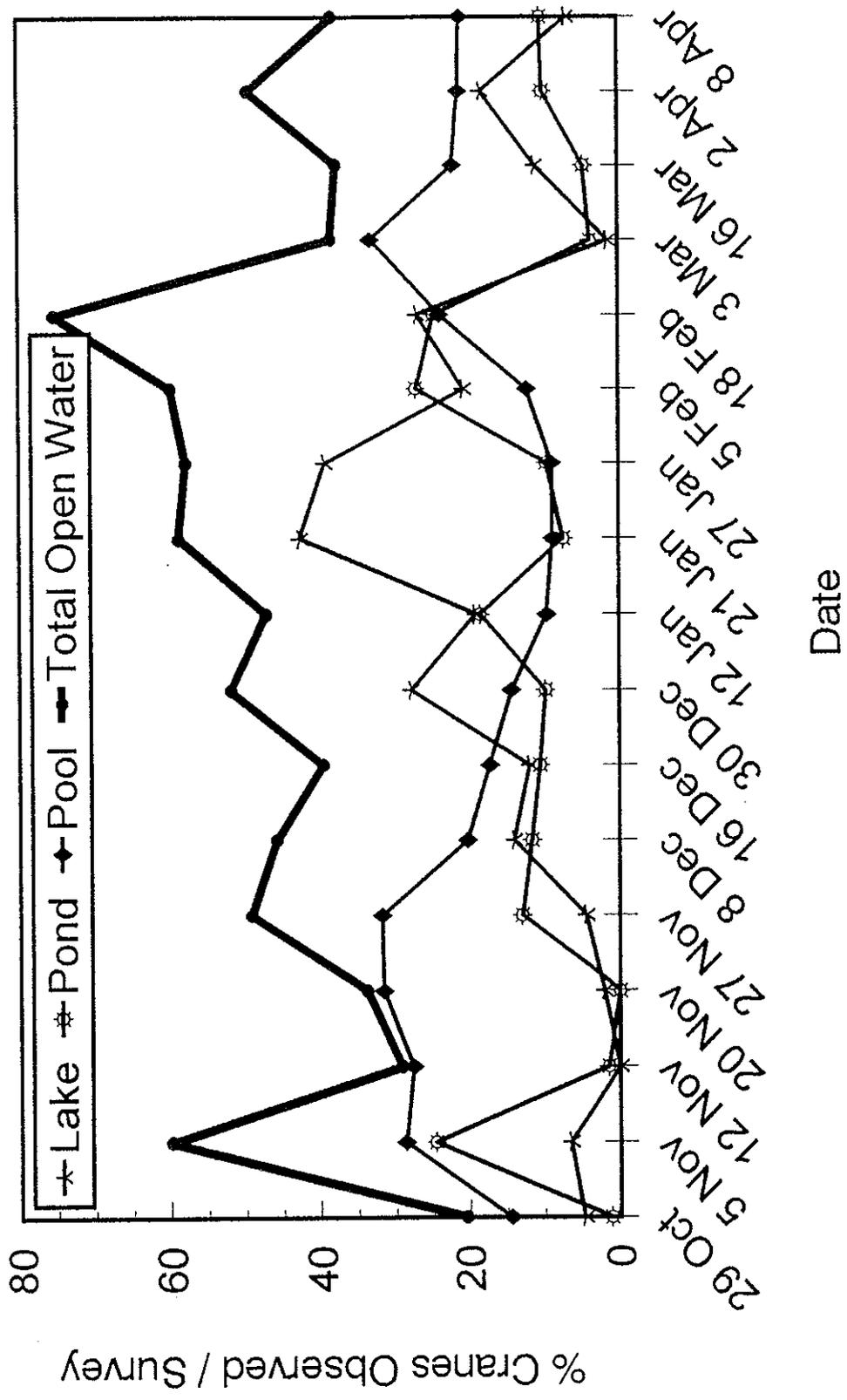


Fig. 4. Proportion of Whooping Crane population observed in different open water habitats of the salt marsh in Aransas and Matagorda Island National Wildlife Refuges during the 1992-93 overwintering season.

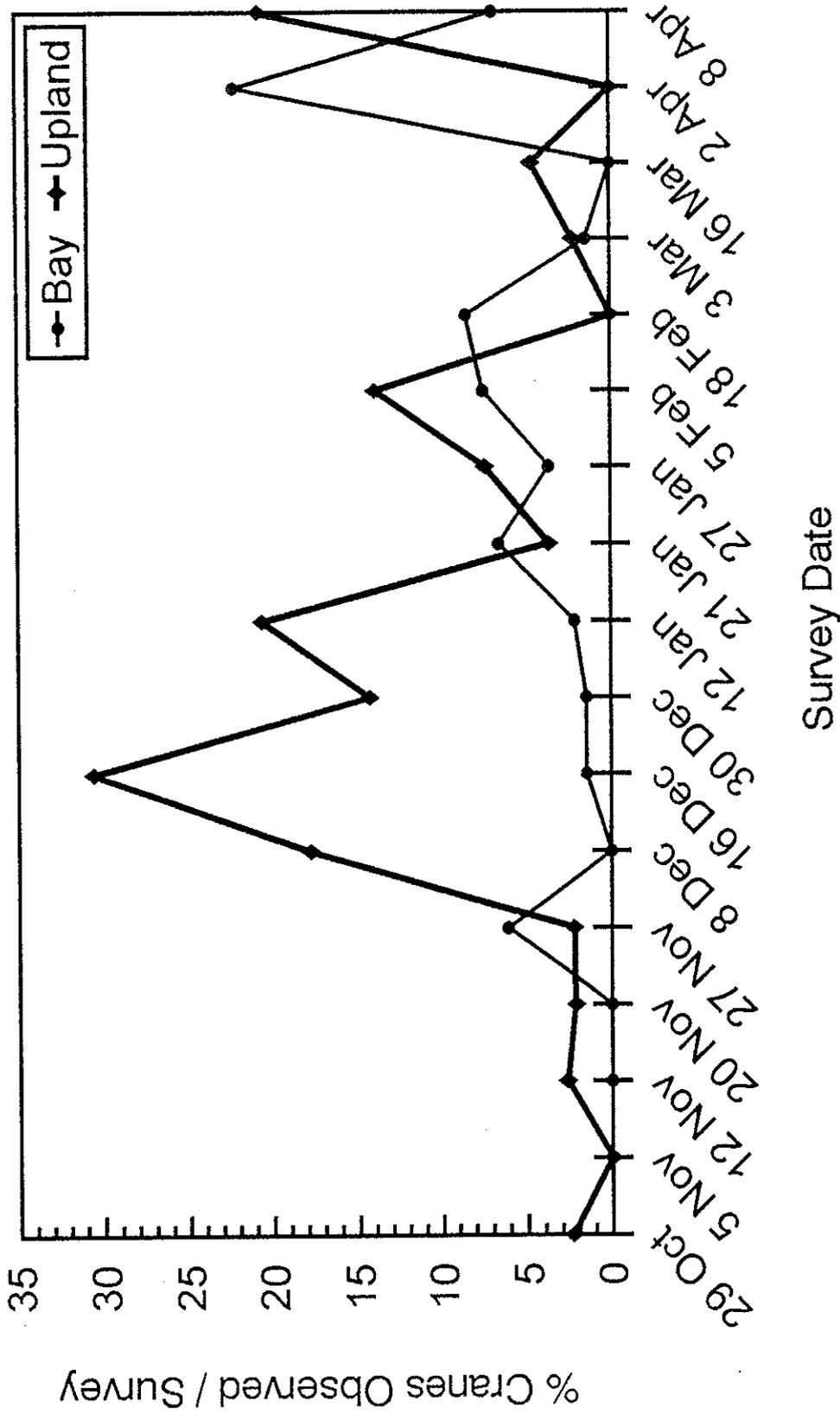


Fig. 5. Proportion of Whooping Crane population observed in bay and upland habitats of Aransas and Matagorda Island National Wildlife Refuges during the 1992-93 overwintering season.

Patterns of habitat use by Whooping Cranes were significantly different among months ($X^2 = 514.03$, $P < 0.001$, $df = 24$; Table 1) during 1992-93 winter. During the month of November 1992 cranes use of specific habitats differed significantly ($X^2 = 735.2$, $P < 0.001$). Salt marsh vegetation and pools were used more than expected, while the remaining habitats were used considerably less than expected. In December 1992, crane use of specific habitats was also significantly different ($X^2 = 90.2$, $P < 0.001$), with vegetation, lake, pools, and uplands used more than expected. In January, habitat use was significantly different among habitats ($X^2 = 164.68$, $P < 0.001$) with lake used considerably greater than expected and vegetation used slightly more than expected. For surveys conducted in February and March habitat use was again significantly different ($X^2 = 174.9$, $P < 0.001$). Vegetation and pools were used significantly more than expected while lakes and ponds were used slightly more than expected. During April, habitat use was significantly different ($X^2 = 31.4$, $P < 0.001$) with pool being used significantly more than expected. Significant differences were also found in pattern of habitat use between the months of December and January of the 1993-94 winter ($X^2 = 514$, $P < 0.001$, $df = 6$; Table 2). During December, use of different habitats was significantly different ($X^2 = 336.6$, $P < 0.001$, $df = 6$) with salt marsh vegetation being used significantly greater than expected (197 vs 65.9) and bay and flats being used less than expected. In January, use of specific habitats was again significantly different ($X^2 = 59.1$, $P < 0.001$, $df = 6$) with salt marsh vegetation again used more than expected, while only bays were used significantly less than expected.

Table 1. Numbers of Whooping Cranes observed in different habitats during different months of 1992-93 winter on the Texas coast.

Month	Habitats										Total				
	Vegetation		Lake		Pond		Pool		Bay			Upland		Other	
	#	%	#	%	#	%	#	%	#	%		#	%	#	%
October	57	68.6	4	4.8	1	1.2	12	14.5	2	2.4	2	2.4	5	6	83
November	255	49.3	17	3.3	49	22	155	29.9	8	3.6	9	4	24	10.8	517
December	81	20.5	71	17.9	42	10.6	68	17.2	4	1	83	21	47	11.8	396
January	68	16.7	137	33.7	48	11.8	37	9	17	4.2	43	10.6	57	14	407
February	27	11.4	57	24.1	61	25.7	44	18.6	19	8	15	6.3	14	5.9	237
March	109	41.9	16	6.2	11	4.2	72	27.7	2	0.7	9	3.5	41	15.7	260
April	23	17.9	20	15.6	13	10.2	30	23.4	24	18.8	6	4.7	12	9.4	128
Total	620	30.6	322	15.9	225	11.1	418	20.6	76	3.7	167	8.2	200	9.9	2028

Table 2. Numbers of Whooping Cranes observed in different habitats during different months of 1993-94 winter on the Texas coast.

Month	Habitats													
	Vegetation		Lake		Pond		Pool		Bay		Upland		Other	
	#	%	#	%	#	%	#	%	#	%	#	%	#	%
October	12	85.7	2	14.3	0	0	0	0	0	0	0	0	0	14
November														
December	197	42.7	46	9.9	62	13.4	70	15.2	18	3.9	42	9.1	26	5.6
January	66	28.6	35	15.2	35	15.2	23	10	6	2.6	22	9.5	43	18.6
February														
March	37	48.6	6	7.8	8	10.5	14	18.4	0	8	10.5	3	3.9	76
April														
Total	312	39.9	89	11.4	105	13.4	107	13.7	24	3	72	9.2	72	9.2

Significant differences were found between winters in a comparison of habitat use patterns during December ($X^2 = 75.1$, $P < 0.001$, $df = 6$) and January ($X^2 = 38.4$, $P < 0.001$, $df = 6$) of the two winter seasons. Greatest differences during the months of December and January occurred in use of salt marsh vegetation which was greater than expected in 1993-94 and less than expected in 1992-93. Upland use in December was greater than expected in 1992-93 and less than expected in 1993-94.

Winter Movements and Sociality.-- There were significant differences in the mean proportion of Whooping Cranes detected per survey compared to total population size ($U = 111.5$, $P < 0.05$) between the two winters. During the first winter a mean of 96.7 % (SD = 2.6, $N = 9$) of the wintering Whooping Crane population was detected during aerial surveys. In 1993-94, however, the mean proportion of cranes detected per survey declined to 89.4 % (SD = 6.1, $N = 7$), suggesting cranes may have moved away from the normal activity range in the salt marsh during the second season. During 1993-94 Whooping Cranes were sighted consistently in upland wetland and grassland areas not frequented during the first winter.

The proportion of Whooping Crane non-family social groups was greater in upland than in salt marsh macrohabitats during both winters ($X^2 = 20.3$, $P < 0.05$ for 1992-93, $X^2 = 23.3$, $P < 0.05$ for 1993-94, Table 3). In marsh habitats, 229 groups (> 2 cranes) were located during the first winter of which 19.2 % (44) were non-family social groups according to my classification. In contrast, nonfamily social groups accounted for 54.3 % (19) of 35 total groups located in uplands (Table 3). During 1993-94 only 13% (10 of 76) of groups detected were non-family social groups in marsh habitats while 75 % (9 of 12)

were non-family social groups in upland habitats (Table 3). There were no significant differences in numbers of social versus nonsocial groups between winters within either salt marsh or upland habitats.

Foraging Behavior -- Probing and progression rates of Whooping Cranes showed differences among different habitats (Table 4). During the 1992-93 winter significant differences ($P = 0.001$) were observed among habitats in progression rates, but not in probing rate ($P = 0.46$). During 1993-94 significant differences were found in progression rates ($P = 0.01$) but not in probing rates ($P = 0.41$) among habitats. No significant differences were found in probing or progression rates between the two winters in salt marsh vegetation or upland habitats. Significant differences were found in both probing and progression rates in bay habitats between winters. In salt marsh open water habitat no significant differences were found in either probing or progression rates between winters. The data for open water habitats, however, shows large variance during both years as a result of temperature-dependent effects on foraging strategy (Chavez-Ramirez and Slack in review). For data pooled by winter over the two seasons there were significant differences in progression rates ($P = 0.0003$) but not in probing rates ($P = 0.76$).

Table 3. Number, size, and, social classification of Whooping Crane groups located in salt marsh and upland habitats on the Texas coast from 1992-94.

	Salt Marsh		Upland	
	1992-1993	1993-1994	1992-1993	1993-1994
Mean Group	3.08	3.09	5.49	4.6
SD	0.37	0.37	3.9	1.6
range	3-6	3-5	3-18	3-9
mode	3	3	3	5
NF* Group	44	10	19	9
(%)	19.2	13	54.3	75
Family Groups	185	66	16	3
(%)	80.3	87	45.7	25
Total Groups	229	76	35	12

* NF = non-family

Table 4. Foraging attributes of wintering Whooping Cranes in different habitats and years on the Texas coast. Numbers are means and standard deviations (SD).

Habitat	1992-1993			1993-1994		
	Probes/min	Steps/min	N	Probes/min	Steps/min	N
Salt marsh Vegetation	6.1(3.2)	29.8(7.9)	22	11.0(7.3)	27.1(10.8)	37
Salt marsh Open Water	24.6(27.3)	14.3(9.6)	19	42.1(31.4)	26.1(13.7)	17
Bay	22.8(6.5)	7.9(13.9)	6	12.2(3.6)	24.1(8.3)	8
Uplands	2.2(0.8)	10.4(7.1)		2.8(1.2)	27.1(3.4)	

Whooping Cranes appeared to forage on a single food item in each marsh habitat during each season (Table 5). During both winters cranes fed on wolfberry while in salt marsh vegetation. In open water habitats cranes were observed to capture and feed primarily on blue crabs. Fish (2 observations) was the only other food item observed taken from open water habitats. While in bays, cranes were observed foraging on dwarf clam during 1992-93 and on razor clams in 1993-94. Whip eels (Bascanichthys scuticaris) were captured on one occasion during November 1993 (Stehn pers. comm.) from bays. While in upland burns, cranes were observed taking a variety of dead or dying prey items including insects in the orders Orthoptera and Odonata, glass lizards (Ophisaurus attenuatus) (5 items), and unidentified snakes (2 items).

Whooping Cranes consumed an estimated 7.1 blue crabs per hr during the first winter compared to 2.8 crabs per hr during the second winter, resulting in a decrease of greater than 50% in mass consumed per hr (Table 5). The number of wolfberries consumed per hr was approximately 30 % greater during the second season, whereas wolfberry mass consumed was 40% greater in 1993-94. While foraging in bays, cranes were estimated to consume 656.6 dwarf clams per hr (252.8 gr/hr) during the first winter and only 12.5 razor clams per hr (22.5 gr/hr) during the second winter (Table 5).

Table 5. Type and quantity of prey items consumed by Whooping Cranes while in different habitats of the salt marsh on the Texas wintering grounds during two winters.

Habitat	Season*	Prey Type	Mean Mass of Item (gr)	Prey Intake Rate	
				# / hr	gr / hr
Salt Marsh	1	Wolfberry	0.46	135.4	62.3
Vegetation	2	Wolfberry	"	231	106.3
Salt marsh	1	Blue crab	98.1	7.1	696.5
Open Water	2	Blue crab	118.8	2.8	332.6
Bay	1	Dwarf clam	0.385	656.6	252.8
	2	Razor clam	260.2	12.5	22.5

* 1 = 1992-93 winter, 2 = 1993-94 winter

DISCUSSION

Habitat Use, Food Use, and Foraging Behavior.-- Habitat use patterns of Whooping Cranes, not surprisingly, appears to be associated with food availability in some habitats. During the winter of 1992-93, surveys were conducted on a regular, nearly weekly schedule. Cranes use of salt marsh vegetation was high early in the wintering period, then declined and remained below 20% from mid- December through March. The decline in use of marsh vegetation in December generally coincided with a sharp decline in the availability of ripe wolfberry fruit. Because of the importance of blue crab in the diet of Whooping Cranes, and the high availability of blue crabs, combined use of all salt marsh open water habitats was high during most of the winter period of 1992-93, ranging from 30 - 60%. The only significant use of bay habitat reflected on aerial surveys occurred at a time of high clam availability. Similar patterns have been reported for other species. For example, Fasola (1994) found that European herons used habitats and prey based on profitability and local abundance of prey items.

Whooping Crane use of upland areas has been reported previously in several works (Allen 1952, Bishop and Blankinship 1982, Bishop 1984, Hunt 1987) as related to availability of acorns (Allen 1952, Hunt 1987, Bishop 1984), wolfberry fruit (Hunt 1987), paspalum grasses (Stevenson and Griffith 1946), and cultivated crops (Shields and Benham 1969). Use of uplands was opportunistic during 1992-93, occurring primarily in areas that had been recently burned and likely in response to readily available and short lived food supplies including dead vertebrates, invertebrates, and selected plant matter (Chavez-Ramirez et al. 1996).

Whooping Cranes appear to be opportunistic feeders. In bay habitat, cranes consumed a different clam species during each year of the study. During the first winter cranes appeared to have responded to an explosion in density of dwarf clam in the bays. Irruption in dwarf clam numbers, with rapid increases in population density in short periods of time, is a common, although irregular occurrence during winter in the Gulf of Mexico (Britton and Morton 1989). During the second winter, dwarf clams were not encountered in significant numbers in bays, and cranes were observed to consume only razor clams while foraging in bay habitat. Razor clams, however, were not collected in sampling efforts, suggesting razor clams were rare in the study area or the sampling technique used was inadequate to detect them.

The significant differences found between winters in bay habitats in both probing and progression rates were likely due to cranes foraging on the different clam species. The number and proportion of cranes observed in bay habitat each season was low, suggesting that over the entire winter period clams were not a significant contributor to the overall crane diets during either winter. Examination of fecal samples collected in 1993-94 supports the low use of clams during that winter (Chavez-Ramirez pers. observ.). The only significant use of bay habitat during any single survey occurred in mid-April 1993 when almost 25% of cranes were observed in this habitat. The unusually high number of cranes observed in bays in April 1993 corresponded to a period of high dwarf clam concentrations encountered in bay habitat and supports the contention that Whooping Cranes are highly opportunistic feeders. Use of specific areas and/or prey with increased densities has been noted in other bird species. Black-tailed Godwits (*Limosa limosa*) have been shown to shift diets in response to increased densities of a bivalve mollusc (Moreira 1994). Wiens and

Rotenberry (1990) have identified high temporal and geographic variability in the diets of granivorous birds. Our data on Whooping Cranes is in agreement with Fasola's (1994) contention that opportunistic use of food resources by birds may be a more common pattern than is widely accepted (Fasola 1994).

The presence and availability of clam species, from year to year in Whooping Crane wintering areas appears to be highly variable and dynamic. In the late 1970's angel wing clam (*Cyrtopleura costada*) appeared to be the most commonly taken clam species from bays by Whooping Cranes at that time (Blankinship pers. comm.). Clam dynamics and species distributions are influenced by a variety of factors, including salinity, temperature, and water turbidity (Holland and Dean 1977, Montagna and Kalke 1992). The use of snails was not documented visually, although plicate horn snail shells were common in Whooping Crane feces collected during the winter of 1993-1994 (Chavez-Ramirez pers. observ.). Because of the lack of live snails located during sampling efforts and the high availability of empty shells, it is possible the cranes were using snail shell as grit material. Snail shells were not broken up significantly in digestion as evidenced by large particles of shells, and some complete shells, found in feces (Chavez-Ramirez, pers. observ.). On two occasions during field observations a pair of cranes was observed picking shells from a mudflat. An examination of the site of shell collection revealed the impression of the shell on the substrate suggesting it was an empty shell and not a live snail.

Based on visual observations and patterns of habitat use, my results are in general agreement with previous studies regarding the importance of blue crab in the winter diet of Whooping Cranes (Allen 1952, Hunt and Slack 1989). Like Hunt and Slack's (1989) results, visual observations of food (and habitat) use also show considerable variability.

Blue crab trapping data suggests that this important food item of Whooping Cranes can become limited in the wintering grounds during some years, which may translate into survival consequences for some individuals (see Chapter IV). Reduced availability of blue crabs during the second year of study resulted in a reduction greater than 50% in blue crab capture rates per hr by Whooping Cranes. The dramatic decrease of blue crab from one season to the next occurred during an extended episode of unusually low tides during August and September of 1993 (Chavez-Ramirez pers. observ.). During the time of low tides water levels declined below the substrate level of most open water areas of the marsh causing extensive mortality of marine life that included crabs and fish.

The reduced availability of blue crab, and consequent low capture rates, during the 1993-94 winter appeared to have been compensated to some degree with an increase in use of other food items, particularly wolfberry. No significant differences were found, however, in probing or progression rates between years in salt marsh vegetation despite the cranes' estimated increased consumption (30% by numbers and 40% in mass) of wolfberry fruit per hr during the second winter. Small changes in foraging rates quantified over short periods can apparently translate into significant differences over longer temporal periods (e.g. hours to a day). This is significant because based on the lack of statistical difference my conclusion would have been that there was no difference in intake rates, when in fact over a day there was as much as a 30% increase in number of wolfberries consumed. The proportion of time spent feeding and in locomotor activities in the salt marsh vegetation, as reflected in time activity budgets, also did not differ between years (Chapter III). Whooping Cranes, however, used salt marsh vegetation more than expected during 1993-94 and less than expected during 1992-93. Together these results suggest that the primary

adjustments made by cranes to increase their use of wolfberry fruit was by increasing the amount of time spent in vegetated habitat rather than by significant increases in the number of fruit consumed per unit time (one minute) or the total time spent in actual foraging activities.

I found no differences in foraging attributes (probing and progression rates) between winters in open water habitats despite differences in crab abundance. The proportion of time spent in foraging activities in open water habitats, based on time activity budget data, also did not differ between winters (Chapter III). This lack of differences, in probing and progression rates, appears to be an artifact of pooling data over a variety of environmental temperatures. Whooping Crane blue crab foraging strategy in open water habitats was found to be dependant on environmental temperature (Chavez-Ramirez and Slack, in review). Water temperature apparently influences activity patterns and visibility of blue crabs since I found them immobile in small depressions at colder temperatures. In laboratory experiments, blue crabs showed significantly less movements per unit time at temperatures below 17° C compared to those above (Harris unpubl. data), with greatest variance observed at temperatures one degree above and below 17° C.

Differences were observed in proportion of cranes using open water habitats between the two winters for the two months (December and January) with equal number of surveys during both years. During December, Whooping Crane use of all open water habitats was approximately 10% greater the first year (47%) than the second year (38.6%), while in January differences were even greater with 57% use of open water habitats the first year and only 40% the second year. Increased use of open water habitats in the first year of the study suggests that cranes modified mesohabitat use patterns, and did not alter their

foraging strategy or increased the amount of time spent in foraging activities while in that habitat. The mechanism by which cranes evaluate and then switch from using low productivity habitats to more productive ones is not known, but may be a response to decreased return rates observed in blue crab captures the second year.

Movements and Sociality.-- Whooping Cranes appear to be more social (likely to associate with cranes other than mates or own young) in upland habitats than in salt marsh areas. This behavior had been noted previously (Bishop 1984) though it had not been quantitatively compared among marsh and other habitats. Species that utilize more than one macrohabitat may show different degrees of sociality, or dispersion, according to prey type found in each habitat (Goss-Custard 1985). In White-faced Ibises (Plegadis chihi), group sizes differed between wetland and grassland habitats (Amat and Rilla 1994). Known distribution of Whooping Crane winter territories is strictly within the salt marsh (Stehn and Johnson 1987, Stehn 1994) and agonistic interactions between conspecifics are rare in habitats other than salt marsh (Chavez-Ramirez unpubl. data). Similarly, White-faced Ibises in Uruguay exhibited territoriality in wetland areas but not in upland sites (Amat and Rilla 1994). Whooping Crane territorial establishment and defense of marsh areas suggests that in most years abundant and defensible resources may be present there (Brown 1964). The degree of territoriality in Whooping Cranes may be influenced by blue crab availability in marsh habitats. The most striking difference in food availability between the two winters of study involved the dramatic difference in numbers of blue crab and reductions in capture rates. Food shortage during the second winter may have been particularly severe when wolfberry fruits became limited after mid-December, prompting

cranes to search for food in other areas with more regularity than during the first winter.

During the 1993-94 winter season, aerial surveys recorded an average of 89.4 % of known wintering population within normal activity range, compared to 96.7% during 1992-93. I interpret this significant difference as increased movement of cranes away from marsh areas during the second year, likely as a result of foraging for food in other habitats. In addition, cranes regularly frequented freshwater areas and other upland habitats during the 1993-94 winter (Chavez-Ramirez pers. observ.). During 1992-93 winter observations of cranes outside the normal range were rare. In addition, increased crane mortality during the second winter may be indicative of food shortages. During 1992-93 winter there were no confirmed dead or missing Whooping Cranes, while in 1993-94 five chick and two subadult mortalities were recorded (Stehn 1994), further suggesting that food limitations may have been a problem. Lack (1966) has proposed that density dependant mortality would be more intense on immature birds, which has been shown to be the case in Great Blue Herons (Ardea herodias) during autumn and winter periods (Butler 1994).

Documentation of increased social interactions in a species which rarely socializes with individuals, other than mates and immediate family members, may suggest increased social facilitation in locating food resources in upland areas. A smaller percentage of social groups were located in salt marsh habitats during the second winter compared to the first winter, while the proportion of social groups in uplands increased during the second year. The lack of statistical significance may reflect the reduced number of surveys conducted during the second winter. On upland habitats territorial behavior is not exhibited and cranes were observed in groups of 28 individuals, including pairs, family groups, and subadults. Social interactions in the form of groups in upland areas may reflect flocking behavior as a

response to changes in resource abundance or availability, such as may occur after prescribed fires facilitate access (Hunt 1987, Chavez-Ramirez et al. 1996). Temporary flocks may increase foraging facilitation at novel sites through increased food intake rates as well as enhanced predator avoidance (Pulliam and Caraco 1984, Carrascal et al. 1993).

Whooping Cranes appear to respond to groups in a way similar to that predicted by local enhancement theories (Crook 1965, Kennedy and Gray 1994) where an individual locates food by joining other members of its group at certain patches. Alonso et al. (1994) report that individual White Storks (*Ciconia ciconia*) and Common Cranes (*Grus grus*) remained in a patch based on the presence of conspecifics in that patch, rather than based on instantaneous food intake rates. While in upland habitats Whooping Cranes showed low probing rates compared to other habitats (Table 4) and time spent in feeding activity was significantly less in upland habitats (10%) compared to all other individual habitats (all >37%) (Chapter III). Reduced probing rates and foraging time suggest high food intake rates was not the primary reason to frequent these sites, unless occurrences at these sites served as scouting visits. In wading birds, Kushlan (1981) suggests that some species use a trial and error approach, visiting sites of low food availability on a regular basis but remaining for extended periods only when food resources increase. Whooping Crane permanence on uplands may follow a pattern similar to that reported for patch use in White Storks and Common Cranes (Alonso et al. 1994).

CHAPTER III

SPATIAL AND INTERSEASONAL EFFECTS ON TIME ACTIVITY BUDGETS OF WINTERING WHOOPING CRANES

SYNOPSIS

I studied time allocation by wintering Whooping Cranes (*Grus americana*) on the Texas coast by constructing time activity budgets to evaluate differences in behaviors due to spatial and yearly differences. Spatial effects were evaluated by comparing time activity budgets between: 1), mainland (Aransas National Wildlife Refuge) and barrier island (Matagorda Island National Wildlife Refuge) birds and 2), between cranes in different habitats (salt marsh vegetation, salt marsh open water, bays, and uplands) within the mainland cranes. Yearly differences were evaluated by comparing activity budgets between two consecutive winters (1992-93 and 1993-94). Mainland and island cranes differed significantly in time spent in maintenance and alert behaviors during the first winter and in time spent in rest and alert behaviors during the second winter. During the first winter, differences were found in proportion of time spent by cranes in all behaviors (feeding, locomotion, interaction, rest, maintenance, and alert) among the four habitats of the mainland. During the second winter there were no significant differences in any of the behavioral categories between habitats of the mainland. Comparisons between years differed depending on habitat investigated. There were no significant differences in proportion of time spent on any of the behaviors in salt marsh vegetation. In salt marsh open water significant differences were found in interaction, maintenance, and alert

behaviors between winters. In bays, interaction and rest differed between years, while in upland habitat only rest time differed. Some differences in time activities are explained on the basis of food availability, disturbances, and possible predation risks associated with different location (mainland vs. island), habitats, and year.

INTRODUCTION

Time and energy are finite resources. The ways in which animals allocate resources will ultimately define individual survival and reproductive success (King 1974, Walsberg 1983). The apportionment of time and energy may be affected by many biotic (body size, species physiology, food availability, competition, and predation) and abiotic (weather) factors (Goldstein 1990, Morse 1990, Morrison et al. 1992). During the nonbreeding season food is the resource of primary importance, and food acquisition should play a prominent role in determining a bird's use of space and time (Hutto 1985). Acquisition of food may be complicated by differences in seasonal availability of food items in different habitat patches (Wiens 1989), as well as by risks of predation associated with different habitats (Caraco 1980, Lima 1993).

An individual must maintain a positive energy balance during the winter season in order to survive. This is accomplished primarily through apportionment of time and appropriate use of space so as to procure sufficient resources to meet immediate energetic needs, and possible excesses to offset future potential negative balances. The winter period in temperate regions, with shorter days and fewer predictable food supplies, may represent a period of food and energy limitation for birds (Weathers and Sullivan 1993). The shortage

of resources during a critical period such as premigration, may affect survival during migration and ultimately reproductive success during the upcoming breeding season. In addition, limited resources, or time in which to obtain them, during any portion of the winter, may affect overwinter survival. Therefore, the amount of time spent foraging generally takes precedence over other behaviors. In order to increase odds of survival, individuals must also spend time looking for predators and responding to disturbance factors that may represent potential survival hazards, sometimes at the expense of foraging time (Lendrem 1983, Lima 1985, Pöysä 1987, Mabit et al. 1989). Birds must, therefore, choose among behaviors with different energetic costs and must obtain sufficient energy to compensate for foraging, alert, and avoidance behaviors plus the cost of other activities, such as maintenance, thermoregulation, storage, and reproduction (Goldstein 1990). An individual that spends little or no time in maintenance and rest activities may suggest that an individual is nearing or in energetic deficit, while, individuals that engage in rest and/or maintenance or other elective behaviors may be indicative of its prior success in procuring sufficient energetic resources (Walsberg 1983).

Studies reporting time activity budgets of birds have generally attempted to address temporal variations between seasons (Weathers and Sullivan 1993), differences within phases of the nesting period (Moreno and Hillstrom 1992), and intraseasonal differences in nonbreeding periods (Alonso and Alonso 1993). Variations in patterns of time activity budgets of birds have not been adequately evaluated with regards to different geographical location or microhabitat, except perhaps in relation to predation risk (Caraco 1980, Lendrem 1983, Metcalfe 1984, Lima 1993). For example, do birds of the same species in

separated geographical locations differ in their time activity budgets? Also, do birds adjust their behavioral activities while foraging in different patches or microhabitats within the same area? While differences are expected, I know of no studies that have attempted to address these concerns in relation to all behavioral categories of time activity budgets. Differences in resource type and abundance between locations and differential predation risks at different sites may result in differences in time activity budgets between individuals occupying those sites.

I studied the allocation of time by wintering Whooping Cranes (*Grus americana*) on the Texas coast by constructing time activity budgets to evaluate differences due to spatial and interannual effects. I evaluated spatial effects by comparing time activity budgets at two scales; 1), between geographic locations, mainland versus barrier island Whooping Cranes; and 2), between individuals in different habitats within the mainland group of cranes. Interannual differences were evaluated by comparing time activity budgets between the two winters during which this study was conducted. Knowledge of factors affecting time activity budgets is of particular importance for the endangered Whooping Crane because in November 1995 only 155 individuals (T. Stehn pers. comm.) survived in the single remaining wild flock of this species. Better knowledge regarding factors affecting feeding and other behavioral activities could help in management and conservation efforts for Whooping Cranes wintering on the Texas coast.

METHODS

This study was conducted on Aransas and Matagorda Island National Wildlife Refuges (ANWR and MINWR, respectively) located on the Texas coast during the months of October through April of 1992-93 and 1993-94. ANWR is located in Aransas and Refugio counties and is approximately 60 km north of Corpus Christi, Texas. MINWR is a barrier island, 62 km long and varies from 1.2 to 7.3 km wide, located in Calhoun county. Matagorda Island is located approximately 7 km east and north from ANWR and generally runs parallel to the coast line of the mainland.

Measurement of behavioral activities of Whooping Cranes took place primarily in the coastal salt marsh portion of the two refuges, which is the primary habitat used by wintering cranes. The salt marsh area is located along the eastern coast of ANWR and on the west side of MINWR. Salt marsh habitats consist of vegetated flats dominated by glasswort (Salicornia virginiana), saltwort (Batis maritima), sea-oxeye daisy (Borrichia frutescens), wolfberry (Lycium carolinianum), saltgrass (Distichlis spicata), and smooth cordgrass (Spartina alterniflora), and wind tidal flats dominated by mudflat grass (Eleocharis parvula), saltgrass, and cordgrasses. Interspersed among vegetated areas are bodies of open water of varying sizes. Behavioral observations were collected from two other habitats used by Whooping Cranes on ANWR, upland sites and bays. Upland habitats are used by Whooping Cranes after recent prescribed fires have been applied and may represent important alternative feeding sites for cranes (Chavez-Ramirez et al. 1996). Cranes also use the shallow portions of bays, up to 80 cm in depth, adjacent to their primary salt marsh habitat.

Behavioral observations were made from blinds and to a limited extent from observation towers, motor vehicles, or boats at ANWR. Observations of Whooping Cranes at MINWR were conducted from boats, motor vehicles and towers. During an observation session, all cranes visible from observation points were sampled once. Each complete observation session lasted between one and six hours depending on number of cranes visible at the time. During observations, focal birds (Altmann 1974) were randomly selected and each was followed visually, with the aid of 10X binoculars or 20-60X spotting scope, for 30 consecutive min. During the 30 min, 120 instantaneous samples were collected by recording the behavior of the crane under observation every 15 sec and classifying each behavior into one of the following categories: feeding, locomotion, maintenance, interaction, alert, and rest. An audio tape was used to give a cue at 15 sec intervals. If the focal crane was lost from sight for longer than five consecutive min the observation session was terminated for that individual. Only focal bird sessions, during which cranes were in sight for greater than 15 min were used in the analysis.

Feeding behaviors were all those involving capture attempts, food item handling, and consumption. Drinking, noted infrequently, was included as feeding. Locomotion involved walking, and with low frequency running and flying, not involved with aggressive or social interaction. Locomotor activity was mostly related to feeding, except during flushing due to a disturbance. Maintenance activities involved plumage maintenance, such as preening, and comfort movements such as, feather ruffling, scratching, stretching, and shaking. Interaction involved activities where an individual reacted to a conspecific by calling or exhibiting agonistic interactions involving movement towards or away from other

cranes. During alert behavior cranes stood with neck straight and head and beak parallel to the ground making a 90° angle (neck and beak). In contrast, during rest behavior the neck showed a distinct curvature and beak was pointed down, the beak and neck made an angle less than 90°. Rest behaviors involved standing, not in alert posture, and sleeping. Cranes exhibiting alert behavior were generally responding to a disturbance by trying to or actually visually locating the source and many times maintaining visual contact for extended periods of time. Disturbances present in the area included aircraft, boats, and barges. In addition, natural disturbances by other animals, some of which were potential predators (Golden Eagles, Aquila chrysaetos, and Bald Eagles, Haliaeetus leucocephala, bobcats, Lynx rufus and coyotes Canis latrans), were present.

Results of behavioral activities are presented as mean proportion of time spent in different behavior activities. A Wilcoxon 2-sample test was used to compare differences in the proportion of time spent on individual behaviors by cranes between ANWR and MINWR, between the same habitat in different refuges, and between the same habitat in different years. A Kruskal-Wallis test was used to compare differences in proportion of time spent in different behaviors among the four different habitats on which time activity budgets were collected on ANWR.

RESULTS

A total of 113 and 92 focal crane observation sessions was conducted in the 1992-93 and 1993-94 winters respectively, representing approximately 55 and 45 hours of time activity budgets. For data pooled across habitats during 1992-93 more time was spent in

maintenance activity at MINWR than at ANWR (11.5% vs 3.6%; $P = 0.004$; Table 6), whereas a greater proportion of time was spent in alert behavior by cranes at ANWR (20.7% vs 11.9%; $P = 0.02$; Table 6). During the 1993-94 winter, differences were found in rest ($P = 0.006$) and alert ($P = 0.04$) behaviors between refuges, with rest being greater on ANWR and alert behaviors being greater on MINWR (Table 6). The data for 1993-94 winter on MINWR reflects observations only from the salt marsh vegetation habitat.

During the winter of 1992-93 significant differences were found in the proportion of time spent in all behaviors (all $P < 0.005$), except locomotion ($P = 0.49$), among the four habitats of ANWR (Table 7). Feeding time was significantly lower in the upland habitat compared to other habitats. The mean proportion of time spent in maintenance activities was less than 0.5% in the two salt marsh habitats of ANWR, while averaging 11.5% in bay and 6.3% in upland habitats (Table 7). Time spent in alert behavior was highest in uplands and lowest in bays while being intermediate and in similar proportion in the two salt marsh habitats. Rest time was low and similar in bay and salt marsh habitats, while being considerably higher in uplands. During the winter of 1993-94 there were no significant differences in any behavior among habitats on ANWR (Table 8). On MINWR in 1992-93 significantly greater locomotor activity ($P = 0.01$) was found in salt marsh vegetation than in salt marsh open water (Table 7).

Table 6. Time activity budgets of Whooping Cranes during winters of 1992-93 and 1993-94 on Aransas and Matagorda Island National Wildlife Refuges. Data represent time activity budgets for all habitats combined for each refuge. Values represent means (SD) of percent time spent in different behaviors, N is number of 30 minute observation sessions.

Behavior	Aransas		Matagorda Island	
	1992-93	1993-94	1992-93	1993-94*
Feeding	35.9(20.3)	36.1(26.9)	36.5(14.5)	31.3(17.7)
Locomotion	32.2(16.1)	33.9(23.5)	34.9(9.8)	38.4(22.3)
Interaction	1.2(1.9)	1(4.4)	0.5(1.5)	2.3(5.1)
Rest	7.6(9.9)	9.8(22.8)	4.8(4.6)	6.6(5.0)
Maintenance	3.6(7.8)	7.6(15.1)	11.5(12.2)	10.3(16.7)
Alert	20.7(14.8)	11.3(11.7)	11.9(6.2)	13.9(9.9)
N	84	64	29	28

* represents data only for salt marsh vegetation habitat

Table 7. Time activity budgets of Whooping Cranes during the 1992-93 winter in different habitats of Aransas and Matagorda Island National Wildlife Refuges on the Texas coast. Values represent means (SD) of percent of time spent in different behaviors.

Location/habitat	Behaviors (%)							N
	Feeding	Locomotion	Interaction	Rest	Maintenance	Alert		
<u>Aransas</u>								
SM Vegetation	37.6(13.9)	35.7(11.9)	0.5(1.1)	3.8(3.2)	0.1(0.3)	22.2(13.7)		16
SM Open Water	44.9(17.4)	31.7(15.3)	1.6(2.1)	4.5(9.7)	0.4(0.9)	18.4(14.8)		34
Bay	47.8(14.5)	28.9(23.4)	0	6.6(8.3)	11.5(13.3)	7.5(6.7)		14
Uplands	10.8(7.9)	32.6(14.8)	1.9(2.4)	16.7(9.8)	6.3(7.9)	32.5(10.4)		20
<u>Matagorda Island</u>								
SM Vegetation	36.5(10.2)	37.4(9.2)	0.6(1.6)	4.1(3.4)	10.4(8.8)	11.2(5.1)		17
SM Open Water	37(28.9)	24.8(2.8)	0	7.8(7.9)	16.3(23.1)	15(10)		12

Table 8. Time activity budgets of Whooping Cranes during the 1993-94 winter in different habitats of Aransas and Matagorda Island National Wildlife Refuges on the Texas coast. Values represent means (SD) of percent of time spent in different behaviors.

Location/habitat	Behaviors (%)							N
	Feeding	Locomotion	Interaction	Rest	Maintenance	Alert		
<u>Aransas</u>								
SM Vegetation	34.6(24.3)	41.8(19.3)	0.9(1.8)	3.3(2.5)	1.3(2.8)	18.3(9.4)	12	
SM Open Water	40.6(28.5)	30.2(26.5)	1.2(5.5)	14.2(27.7)	7.2(16.3)	6.8(8.1)	32	
Bay	29.8(23.5)	38.7(12.4)	1(0.9)	1.5(1.6)	14.5(19.1)	14.5(16.2)	12	
Uplands	12.5(9.8)	41.3(16.7)	0	1(0.8)	13.5(9.8)	29(12.7)	8	
<u>Matagorda Island</u>								
SM Vegetation	31.3(17.7)	38.4(22.3)	2.3(5.1)	6.6(5.0)	10.3(16.7)	13.9(9.9)	28	

There were no significant differences in time spent in behaviors in salt marsh open water habitats ($P > 0.09$) between the two refuges, while in salt marsh vegetation significant differences were found in maintenance ($P = 0.0009$) and alert ($P = 0.01$) behavior between ANWR and MINWR for 1992-93 (Table 7). The mean proportion of time spent in alert behavior on ANWR was double that of the cranes from MINWR. During the second winter significant differences were found only in rest activity ($P = 0.006$) between Aransas and Matagorda Island cranes in salt marsh vegetation, averaging twice as high on Matagorda (Table 8).

A comparison of time activity budgets within the same habitat on ANWR during the two winters yielded mixed results for different habitats. In salt marsh vegetation, there were no significant differences (all $P > 0.15$) in any of the behaviors between the two years (Table 7 and 8). In salt marsh open water, significant differences were found in interaction ($P = 0.001$), maintenance ($P = 0.01$), and alert ($P = 0.0001$) behaviors (Table 7 and 8). Interaction and alert activities were greater during the first winter, while maintenance activity was greater during the second winter. In upland habitat, rest activity was the only behavioral category that differed between winters ($P = 0.0025$), showing a decrease from approximately 16% in the first year to 1% during the second (Table 7 and 8). While in bay habitats, interaction ($P = 0.001$) and rest ($P = 0.03$) behaviors differed between winters (Table 7 and 8). Interaction time increased the second winter in bays, while time spent in rest activity decreased considerably from the first to second winter.

DISCUSSION

Spatial Effects.-- Despite the distance between ANWR and MINWR (approx. 5 km) and the potentially significantly different types and frequencies of disturbances, there were some remarkable similarities in the proportion of time spent in behaviors between the two refuges. For example, time spent feeding and in locomotion was almost identical for Whooping Cranes in the two areas during 1992-93. This suggests that cranes, at least during the first year, required similar feeding time and locomotor effort to obtain sufficient food resources on both ANWR and MINWR. However, maintenance and rest behavioral categories differed significantly during the first year between refuges. Maintenance time was almost three times greater on MINWR, while, alert was almost twice as much in ANWR. If only salt marsh habitat of Aransas is considered in the comparison, the differences are even greater, with maintenance considerably greater on Matagorda (11.5 vs. 0.5%), while alert was more than three times greater on Aransas (40.6 vs. 11.9%).

The highly significant differences in maintenance and alert behaviors between cranes in Aransas and Matagorda Island could be attributable to the greater disturbance regime (frequency and intensity) on Aransas due to the Gulf Intracoastal Waterway (GIWW). The GIWW is responsible for a considerable amount of disturbance in the form of boat and barge traffic primarily, but also as an access lane that allows fisherman and crabbers to move into Whooping Crane territories. In addition, aircraft are common over and near Aransas while rare over Matagorda Island (Chavez-Ramirez pers. observ.). Whooping Cranes are reported to respond, by increasing time spent on alert behavior, to human (airboats, fishermen, and hunters) disturbances on Matagorda Island (Mabie et al. 1989).

Greater alert behavior in ANWR may be due to a greater predation risk associated with the mainland, particularly bobcats which have been implicated in several mortality events on ANWR. Bobcats are rare on MINWR while abundant and commonly seen on ANWR. The result of increased time spent in alert behaviors suggests that Whooping Cranes on Aransas have reduced time to engage in maintenance activities because of regularly having to respond to disturbances from the GIWW.

Assuming the overriding concern of cranes is to meet their daily energetic needs during the time available for foraging during a day, as in other species (Walsberg 1983, Moreno and Hillstrom 1992), Whooping Cranes are expected to partition and prioritize use of available time spent on different behaviors. Walsberg (1983) states, that for energy budgets, allocation of energy to obligatory demands may decide the amount of energy available for expenditure in elective behaviors or activities. Whooping Cranes, therefore, should use available time in a way that will assure sufficient time is spent securing food resources to meet energetic and nutritional needs (obligatory activities, *sensu* Walsberg 1983). In this study, obligatory activities to secure food included feeding and locomotion categories, since much locomotor activity appears to be directly related to searching for food. Time spent in vigilance is considered costly and time spent scanning for predators is considered a tradeoff with energy that would be gained if that time were spent foraging (Lendrem 1983, Metcalfe and Furness 1984). Alert behavior and consequent detection of potential survival hazards, such as predators, is important and must occur whether or not daily energetic concerns are met. I therefore, consider alert also as an obligatory activity. Rest and maintenance activities are considered electives (*sensu* Walsberg 1983). For

example, a crane should spend time in rest and/or maintenance only if survival is assured (predator detection and avoidance and daily energetic needs are, or will be met).

During 1992-93, the sum of obligatory activities (feeding, locomotion, and alert behaviors) for Whooping Cranes in salt marsh habitats of ANWR added up to 95.5% of total time budget, while on MINWR the sum was only 88.3 %. These differences suggests that Whooping Cranes on ANWR have very little time remaining in their daily time budgets to devote to elective activities, while Whooping Cranes on MINWR have considerably more time available to dedicate to elective activities (e.g., rest and maintenance). Alonso and Alonso (1993) report that increases in rest and other nonforaging activities in Common Cranes (*Grus grus*) were due to decreased food availability and/or possibly satiation. The results of the second year, however, at first appear not to be consistent with expectations following the first winter, since alert time was slightly greater and maintenance only slightly higher on Matagorda Island when considering pooled data. As reported earlier, however, pooled data for Matagorda Island for the 1993-94 season reflects only data collected in salt marsh vegetation. Therefore, when considering only salt marsh vegetation habitats between refuges the trend in maintenance and alert behaviors observed during the first winter is maintained in the second winter. Except for rest behavior (MINWR > ANWR), no differences in individual behavioral categories for the two sites were found.

Among Habitat Effects.-- Different patterns in use of time in each habitat may not be surprising considering that each habitat provides Whooping Cranes with different prey items (Chapter II) and possibly has a different predation risk associated with each as well.

Whooping Cranes used different habitats in different ways as reflected by differences in all behaviors, except locomotion, between habitats of ANWR during the 1992-93 season. Feeding was high in all habitats (> 37%) except in upland burn habitats (10.8%), while resting activities were more than twice as high in cranes present in uplands than in any other habitat. The significantly greater time spent in alert behavior on upland and significantly less time in alert in bay habitat than all other habitats, may reflect differential predation risk associated with each habitat. Although, adult wild Whooping Cranes may have few predators on the wintering grounds and effects of predation on the population may be negligible, the "effect" of predators (sensu Lima 1993) on crane habitat selection, foraging, and time activity budgets may be very important. Several confirmed killings of Whooping Cranes during the winter have been documented on ANWR, the last of which occurred during the 1993-94 winter. Increased alert behavior in uplands may be a consequence of Whooping Cranes' perception of predator risk when away from salt marsh areas. Feeding Eurasian Widgeons (*Anas penelope*) perceive greater predation risk as feeding site distance increased from water's edge (Mayhew and Houston 1989). Wild Whooping Cranes are believed to roost almost exclusively in open water habitats, suggesting a perceived feeling of security and indicating that a greater probability of predator detection is associated with this type habitat.

Whooping Cranes spent the least time in alert behavior while in bay habitat, which is surprising since the bay areas of ANWR are the habitats closest to the GIWW. One would expect that proximity to watercraft traffic would have imposed greater vigilance activity in the cranes as reported by Mabie et al. (1989). The possibility exists that ANWR Whooping

Cranes have become habituated to constant traffic of the GIWW and no longer perceive activity on it as a threat. The cranes studied by Mabie et al. (1989) were on MINWR where boat disturbances are considerably less frequent. Lowered alert time in bay, however, may reflect perceived lower predation risk by cranes in this habitat. Perhaps the observed pattern of Whooping Cranes alert behavior mirrors that described for shorebirds (Metcalf 1984) and Rheas (Martella et al. 1995) which exhibited increased vigilance (alert) time in habitats with less visibility. If this is the case, I would expect Whooping Cranes to show alert behavior from highest to lowest in the following manner; uplands > salt marsh vegetation > salt marsh open water > bay. My data for the first winter support the theory of increased vigilance in habitats with reduced visibility, while data for 1993-94 is only partly consistent with expectations (Tables 7 and 8).

During the 1993-94 winter season there were no significant differences in any of the behaviors among habitats in Aransas. However, Whooping Cranes in uplands again showed low feeding activity and a high proportion of time in alert behavior (Table 8) and with those in bays showed greater maintenance than in the two salt marsh habitats. Upland habitats may be used for purposes other than obtaining food resources. In effect, Aransas Whooping Cranes on uplands forage less, rest more, spend more time in alert, and socialize extensively (Chavez-Ramirez et al. 1996). While in uplands cranes tended to congregate in groups greater than any encountered in marsh areas (Chavez-Ramirez et al. 1996). Flock formation in uplands is unusual behavior since on the wintering grounds Whooping Crane pairs and family groups maintain and defend territories. The low feeding time in uplands suggests social facilitation, with cranes responding to presence of other cranes rather than

to actual food intake rates experienced in the habitat. Alonso et al. (1994) report that permanence time in a patch by individual White Storks (Ciconia ciconia) and Common Cranes is based on group size rather than on food intake rate *per se*.

Between Year Effects.-- Differences in time activity budgets of Whooping Cranes within the same habitat between winters showed no significant differences in some habitats while considerable differences were found in other habitats. No significant differences were found in any of the behavioral categories in salt marsh vegetation between winters with the greatest numerical change being a 6% increase in locomotion the second year. This may not be surprising considering the fact that food (wolfberry) availability and phenology were similar between years in this habitat (Chapter II).

The decrease in alert behavior in Whooping Cranes in open water habitats, though not intuitive, is consistent with the situation reported in the literature. Greatest differences between years were present in salt marsh open water habitats where interaction time decreased, maintenance time increased, and alert times decreased from 1992-93 to 1993-94 season. Surprising results are the increased maintenance and decreased alert behavior in this habitat, but not in salt marsh vegetation since they are both parts of crane territories and could be considered patches of the same habitat. Decreased alert time is unusual, and previous studies have reported decreased vigilance time in other bird species as foraging demands increased. Teal (Anas crecca) for example, sacrificed vigilance as foraging demands increased (Pöysä 1987) and blackbirds (Turdus merula) foraging on cryptic prey were less vigilant than those foraging on conspicuous prey items (Lawrence 1985). Food

availability (blue crab) decreased significantly in salt marsh open water habitats from first to second year, which consequently translated into a reduction of greater than 50% in blue crab capture rates during 1993-94 (Chapter II). Similarly, Common Cranes showed increased time spent in rest and other nonobligatory activities despite decreased intake rates between two winter periods (Alonso and Alonso 1993). Larger species tend to suffer less predation risk (Illius and Fitzgibbon 1994) than smaller species. In Whooping Cranes, which can be greater than 1.5 m tall, predation may have played a major role in selecting for adaptive foraging strategies over time on the wintering grounds, even if the net effect of direct predation is small (Lima 1993). If this were true, the consequences (kill by predator) of reduced time spent in alert behavior during periods of food stress may be minimal, allowing such a species to reduce vigilance time to increase time spent in searching for and acquiring food resources during periods of low food availability.

The increase in maintenance (and numerically also rest) activity from first to second season in open water habitat, when food resources in this habitat were reduced in 1993-94 relative to the first season, is puzzling. I expected a decrease in elective behaviors and an increase in obligatory activities compared with the first season, yet the opposite trend was observed. It appears that the proportion of the time budgets saved by reducing alert behavior time was used in elective rather than obligatory activities as expected.

In bay habitat only time spent in interaction and rest behaviors differed statistically between years, despite large numerical differences in mean proportion of time spent in other behaviors. For example mean feeding time decreased from 47.8% to 29.8% and locomotion increased from 28.9% to 38.9% from first to second winter. Whooping Cranes

foraged on a different food item each year in bays, dwarf clam in 1992-93 and razor clams in 1993-94, which exhibited different distribution patterns and apparent densities (Chapter II). Dwarf clams were highly clumped and found in high densities on or near the substrate surface, while razor clams dig deep into sediment and apparently are found in low densities (although this was not quantified in this study). Numerical differences in feeding and locomotion were, therefore, expected. Reduced foraging (feeding and locomotion) and alert behaviors during the first season were expected to have been reflected as an increase in elective activities which was shown for rest but not maintenance behavior.

CHAPTER IV

TEMPORAL PATTERNS IN ENERGETIC BUDGETS OF WINTERING WHOOPING CRANES

SYNOPSIS

I evaluated the energetic budgets of nonbreeding Whooping Cranes on the Texas coast during the months of October-April during 1992-93 and 1993-94 winters. I compared energy budgets among different months and between the two winters. Energy balance of cranes was evaluated by comparing estimates of daily energy expenditure (DEE), based on time activity budgets, with estimates of daily energy intake (DEI), based on food consumption rates and energetic value of foods. I determined the energetic contribution of the different food items to the daily and overall winter diets and energy intake of Whooping Cranes. Overall mean daily DEE per month was not significantly different ($P > 0.05$, $U = 24$, $df = 4, 7$) during the two winters of study. However, gross energy intake was significantly less during the 1993-94 winter ($P = 0.01$, $U = 11$, $df = 4, 7$). During 1992-93 Whooping Cranes showed a consistently high positive energy balance during all months. During 1993-94 crane energy budgets were negative during October and December (no data for November), slightly positive in January (+126 kJ) and significantly more so in March (+889 kJ) (no data for February). The most significant source of energy for Whooping cranes was blue crab during both winters. During 1992-93 blue crabs contributed between 62% and 98% (mean 88.4) of energy intake during all winter months, while during 1993-94 they contributed between 18% and 97% (mean = 58.8%) during the different months. Wolfberry was the second most important source of energy for cranes

contributing between 36%, 17%, and 10.7% during October through December 1992, respectively. During the 1993-94 winter wolfberry contributed between 33.3% and 81.6% during the different months (October - January, excluding November). I used daily energy budgets to evaluate predictions regarding overwinter survival and reproductive success during the two winters in relation to the amount of potential energy stores during the two different years of study.

INTRODUCTION

During the non-breeding season food is the resource of primary importance, and the acquisition of food should play a prominent role in determining a bird's use of time (Hutto 1985). Because different behaviors have varying energetic costs (Goldstein 1990) overall time activity budgets will ultimately determine energetic budgets. Individuals must maintain a positive energy balance during the winter season in order to survive. This is accomplished primarily through apportionment of time so as to procure sufficient resources to meet a day's energetic needs and possibly exceed daily needs to store as reserves to offset future potential negative balances during a day. For example, in cold weather, fat reserves are deposited during the day to compensate for losses that may occur during the night (Kendeigh et al. 1977).

Acquisition of food, and ultimately energy, may be complicated by seasonal availability and distribution patterns of food items and predation risks (Lima 1993). During the non-breeding period time and energy budgets may vary between phases of the yearly cycle in some bird species (Alonso and Alonso 1993), such as between migration and

wintering periods. Variations may also occur within a single season, such as among early (after arrival in wintering ground), mid, and late (premigration and possibly pre-breeding) periods within the winter. During particular phases of the wintering period use of energy for maintenance versus maintenance and energy storage may vary. For example, prior to migration birds may be more likely to be concerned with storing reserves for migration and possibly breeding than just simply meeting daily energetic needs (McLandress and Raveling 1981).

Energetic requirements to endure migration and subsequent reproduction upon arrival on breeding grounds are considered to be high in some species (Kendeigh et al 1977, Ankney and Alisauskas 1991). The shortage of resources during a critical period, such as premigration, may affect survival during migration and may affect reproduction during the upcoming breeding season. Reproductive success may depend on the accumulation of adequate energy reserves on the wintering grounds (McLandress and Raveling 1981, Joyner et al. 1984). More directly, however, a limited availability of resources or time in which to procure them, during any portion of winter, may directly affect overwintering survival and overall fitness. Winter survival is the major fitness component of many temperate dwelling species during the nonbreeding period (McNamar and Houston 1986, Rogers and Smith 1993).

In temperate regions many overwintering bird species deposit fat reserves during winter (Lehikoinen 1987, Blem 1990) which requires that birds consume energy in quantities greater than their daily energy expenditure (DEE). In Maine, body fat has been reported to have a significant effect on the overwintering survival capacity of Black Ducks

(*Anas rubripes*) (Reinecke et al. 1982). In many Northern Hemisphere bird species the mean mass of individuals has been reported to peak during midwinter (Kendeigh et al. 1977, Lima 1985). In general among bird species, 70-90% of the weight and mass gains observed are the result of increases in fat stores (80-90, Reinecke et al. 1982,). In several migratory crane species, a weight gain as high as 30% of body weight has been observed prior to (Swengel 1992), or during, spring migration (Krapu et al. 1985). The amount and timing during which fat reserves are deposited is believed to represent a tradeoff between risk of starvation and risk of predation (Lima 1985). Reproductive success of many migratory bird species may depend on the accumulation of sufficient energy reserves while on the wintering grounds (McLanndress and Raveling 1981, Williams and Kendeigh 1982, Joyner et al. 1984). Energy reserves obtained in wintering areas sustain northern nesting geese between the time of arrival and nest initiation during years of delayed snow melt (Davies and Cooke 1983). The large energy stores reported for cranes (Krapu et al. 1985, Swengel 1992) may serve a similar function as in geese.

Foraging birds must choose among behaviors with different energetic costs and must acquire sufficient energy to meet both these costs and cost of other activities, such as maintenance, thermoregulation, storage and reproduction (Goldstein 1990). Estimates of DEE have been used extensively in recent years for many bird species in order to evaluate energy budgets using doubly labeled water, feces collection, and time activity budgets (Goldstein 1988, Nagy 1989).

To estimate DEE using time activity budgets it is necessary to determine the amount of time spent by an individual during a day in different activities (feeding, walking, alert,

etc.) and to know the energetic costs of the different behavioral activities of birds under investigation (Goldstein 1988, 1990). There are more direct approaches for arriving at daily energy expenditures in free living birds, however, these methods require capturing and handling of the individuals under study. The time activity budget method unlike other methods has the advantage of being easy to apply in the field, is of low cost, and most importantly is nonintrusive (Nagy 1989). Therefore, the time activity budget method is particularly well-suited for use with endangered species. Endangered populations are generally in low densities and capture and handling of even a single individual poses a considerable risk. Time activity budget methods, however, do require certain assumptions to be made and the use of data on cost of activities that, in most cases, has been collected from other species or populations different from the one under study. Therefore, time activity budgets are likely the best approach for nonintrusive evaluation of DEE of endangered populations and has been shown to be reliable in many instances (Goldstein 1988).

In this study, I evaluate the energetic budgets of nonbreeding Whooping Cranes on the Texas coast during the months (October-April) of their overwintering period and compare monthly and overall energetic budgets between two different winters. I evaluated energy balance of cranes during the wintering months and between years by comparing estimates of DEE, based on time activity budgets, with estimates of daily energy intake (DEI) and energy retained. I evaluated the energetic contribution of different food items to the daily and overall winter diet of Whooping Cranes. Differential daily energy budgets (DEB) and potential for energy storage was used to evaluate predictions regarding

overwinter survival and reproductive success during different years of study.

METHODS

This study was conducted on Aransas and Matagorda Island National Wildlife Refuges (ANWR and MINWR, respectively) located on the Texas coast during the months of October through April of 1992-93 and 1993-94. ANWR is located in Aransas and Refugio counties and is approximately 60 km north of Corpus Christi, Texas. MINWR is a barrier island, 62 km long and varies from 1.2 to 7.3 km wide, located in Calhoun County. MINWR runs parallel to the coastline and is east and north of ANWR. Our study of crane time activity budgets took place primarily in the salt marsh portion of the two refuges, which is the primary habitat used by wintering cranes (Chapter II). The salt marsh area is located along the eastern coast of ANWR and on the west side of MINWR. Salt marsh habitats consist of vegetated flats dominated by glasswort (*Salicornia virginiana*), saltwort (*Batis maritima*), sea-oxeye daisy (*Borrichia frutescens*), wolfberry (*Lycium carolinianum*), saltgrass (*Distichlis spicata*), and smooth cordgrass (*Spartina alterniflora*), and wind tidal flats dominated by mudflat grass (*Eleocharis parvula*), saltgrass, and cordgrasses. Interspersed among vegetated areas are open water bodies of varying sizes. Time activity budgets were also collected from two other habitats on Aransas, upland burn sites and bays. Upland habitats are used by Whooping Cranes primarily just after a prescribed fire has been applied and may represent important alternative feeding sites for cranes (Chavez-Ramirez et al. 1996). Cranes also use the shallow portions of bays adjacent to their primary salt marsh habitat.

Habitat use patterns of Whooping Cranes were determined from aerial surveys by locating the maximum number of individual cranes during near weekly surveys during 1992-93, but due to logistical problems, less intensively and irregularly during 1993-94 (Chapter II). I combined surveys conducted during the same month and used total number of observations to infer habitat use patterns of Whooping Cranes for each month. For this study I assumed that the distribution of cranes (proportion in different habitats) during aerial surveys reflected the patterns of daily use by individual cranes.

Behavioral observations were collected from blinds set adjacent to Whooping Crane territories in ANWR, however, because of the larger territory sizes in MINWR setting blinds was not a feasible option there. Most behavioral observations on MINWR, and to a limited extent in ANWR, were collected from observation towers and vehicles. During an observation session all cranes visible from observation points were sampled once. Observation sessions lasted between 1 and 6 hr depending on number of cranes visible at the time. During observations, focal birds (Altmann 1974) were selected for observation. Each focal bird was followed visually with aid of binoculars or spotting scope for 30 consecutive min. During the 30 min, 120 instantaneous samples were collected by recording behavior of crane under observation every 15 sec in one of the following categories; feeding, locomotion, maintenance, interaction, alert, and rest. A more detailed description of individual behaviors is reported elsewhere (Chapter II). An audio tape was used to give a cue at 15-sec intervals. If a crane was lost from sight for longer than 5 min the observation session was terminated for that individual.

Daily Energy Expenditure. -- The potential total daily energy expenditure (DEE) of Whooping Cranes was determined by the sum of costs, as multiples of basal metabolic rate (BMR), of different behavioral activities. Costs of individual behavioral activities have been previously determined with estimates based on other nonpasserine bird species (Table 9; Bamford and Maloiy 1980, Goldstein 1988). No data is available on exact cost of behavioral activities for Whooping Cranes.

In order to use allometric equations it is necessary to know the mass of the species under investigation. Though the available data is limited for wild cranes, the average weight of a Whooping Crane in the wild has been reported as 7 kg (Johnsgard 1983, USFWS 1986). I therefore, estimated BMR for cranes based on the assumption that wild Whooping Cranes in the study area all have an average mass of 7 kg. I then used Aschoff and Pohl (1970) allometric equations for nonpasserine birds to arrive at estimates of the resting and active BMR in kJ d^{-1} as follows:

$$\text{Resting BMR:} \quad 307.0 M^{0.734}$$

$$\text{Active BMR:} \quad 381.0 M^{0.729}$$

where M is equal to the mass of bird in kg.

Table 9. Behavior categories used in this study and energy expenditure coefficients (EEC) used to estimate daily energy expenditure (DEE) of Whooping Cranes wintering on the Texas coast.

Behaviors	EEC	Reference
Foraging	1.95	Goldstein 1990
Walking	3	Bamford and Maloiy 1980
Flying	11	Goldstein 1990
Resting	1	"
Comfort	1.95	"
Agonistic	2.9	"
Interaction	2.9	"
Alert	2	"

Estimates based on allometric equations used here have been previously evaluated and found to yield results comparable to more direct methods (feces collection) of DEE estimates done on captive Whooping Cranes (Nelson 1995). Daylight behavioral activities were modeled based on 11.45 hr, which was the average daylight length at the study area during the study period. I calculated overnight energy expenditure based on the assumption that all nocturnal activity was resting during the 12.55 hr of dark. Because of the endangered status of the Whooping Crane, and extreme low numbers present on the wintering grounds, more direct methods of estimating DEE in wild Whooping Cranes were not feasible.

More accurate estimates of DEE, over a 24- hr period, can be arrived at with time activity budget data if thermoregulatory costs are considered (Goldstein 1988), particularly if ambient temperature drops below a species' lower critical temperature (Buttemer et al. 1986, Nagy 1989). Time energy budgets (TEB) constructed using allometric equations work best if birds do not show daily behavioral changes for thermoregulation. The predicted lower critical temperature for a 7 kg non-passerine bird based on allometric equations of Calder and King (1974) is -13.5°C . In the study area the temperature over the two winters of study never dropped below -2°C , and it is therefore assumed that any additional energy costs of thermoregulation by Whooping Cranes during the two winter periods on the Texas coast was minimal during the study. In general, it is expected that large birds are less sensitive to their thermal environment and estimates of DEE based on activity budgets may be more accurate for larger species (Nagy 1989).

DEE of Whooping Cranes was determined with the following formula:

$$\begin{aligned} \text{DEE}_{\text{total}} = & (\text{DEE}_v)(P_v) + (\text{DEE}_{ow})(P_{ow}) + (\text{DEE}_b)(P_b) + (\text{DEE}_{ul})(P_{ul}) \\ & + (\text{DEE}_{\text{night}})(P_n) \end{aligned} \quad (1)$$

where:

$\text{DEE}_{\text{total}}$ = Daily energy expenditure in 24-hr period

DEE_v = Energy expenditure in salt marsh vegetation kJ hr^{-1}

DEE_{ow} = Energy expenditure in salt marsh open water kJ hr^{-1}

DEE_b = Energy expenditure in bay kJ hr^{-1}

DEE_{ul} = Energy expenditure in upland kJ hr^{-1}

$\text{DEE}_{\text{night}}$ = Energy expenditure during nighttime hours kJ hr^{-1} , nighttime hr = 12.5

P_x = Proportion of daylight hours spent in habitat x, total daylight hr = 11.5

DEE for each habitat was calculated as:

$$\begin{aligned} \text{DEE}_x = & F_x(\text{xBMR})(P_f) + L_x(\text{xBMR})(P_L) + I_x(\text{xBMR})(P_I) + R_x(\text{xBMR})(P_R) + \\ & A_x(\text{xBMR})(P_A) + M_x(\text{xBMR})(P_M) \end{aligned} \quad (2)$$

where:

DEE_x = Energy expenditure in habitat x in $\text{kJ}\cdot\text{h}^{-1}$

F_x = Time spent in feeding activity in habitat x in hr

L_x = Time spent in locomotor activity in habitat x in hr

I_x = Time spent in interaction activities in habitat x in hr

R_x = Time spent in rest activities in habitat x in hr

A_x = Time spent in alert activities in habitat x in hr

M_x = Time spent in maintenance activities in habitat x in hr

xBMR = Cost of activity as multiple of BMR (basal metabolic rate) $\text{kJ}\cdot\text{hr}^{-1}$ for 7 kg bird

active BMR = $65\text{ kJ}\cdot\text{h}^{-1}$ (Table 9)

Energy Consumption.-- The abundance of different food items was monitored throughout the wintering period (Chapter II). Food intake rates (gr/hr) for specific food items was the sum of food items ingested per unit time multiplied by the mean weight of the food item determined from sampling. The number of food items consumed was determined by counting the number of items taken by cranes per 4 min observation sessions for wolfberry, dwarf clams, and possible insects. Numbers of blue crabs and razor clams consumed were determined by counting the number taken over 30-min periods during which time behavioral data were collected, because cranes could take several minutes to find and consume crabs and razor clams. Energy intake rate for each food item was determined based on the number of food items consumed per unit time and the mean (wolfberry, dwarf and razor clams) or mode (blue crab) weight of individual food items multiplied by the gross energy content of each food item. Gross energy content and metabolizable energy coefficients

(MEC) for most food types (blue crab, wolfberry, clams) were obtained from Nelson (1995) based on studies of captive Whooping Cranes (Table 10). Energy and MEC for other foods (crickets) were obtained from Karasov (1990) (Table 10).

Table 10. Gross energy content and metabolizable energy coefficients for Whooping Crane foods from Texas wintering grounds on dry matter basis.

Food	Gross Energy kj/gr	Metabolizable Energy Coefficient	Reference
Blue crab	11.9	0.36	Nelson 1995
Wolfberry	21.5	0.44	" "
Clams	1.9	0.75	" "
Crickets	22.2	0.74	Karasov 1990

Daily energy intake for Whooping Cranes was determined with the following formula:

$$DEIt = (DEIv) + (DEIow) + (DEIb) + (DEIul) \quad (3)$$

where:

DEIt = Total daily energy intake

DEIv = Daily energy intake in salt marsh vegetation

DEIow = Daily energy intake in salt marsh open water

DEIb = Daily energy intake in bays

DEIul = Daily energy intake in uplands

Energy intake in each habitat was determined with the following formula;

$$DEI_x = (MC \text{ gr.hr}^{-1}) (GE \text{ kj.gr}^{-1}) (MEC_x) (P_x) \quad (4)$$

Where:

DEI_x = Daily energy intake in habitat x.

MC = Mass consumed in gr.h⁻¹ on dry matter basis.

GE = Gross energy content of food in kj.gr⁻¹ on dry matter basis.

MEC_x = Metabolizable energy coefficient for food consumed in habitat x.

P_x = Proportion of daylight hours spent in habitat x.

Energy Balance Model Assumptions.-- I assumed and modeled all activities conducted during the 11.45 daylight hours under the active BMR (65 kJ hr^{-1}), while all nocturnal behavior was assumed to be resting and modeled under resting BMR (56 kJ hr^{-1}). The daily energy balance of Whooping Cranes is based on the difference between total metabolized energy intake and daily energy expenditure as calculated by equations (3) and (1). I did not assume that Whooping Cranes had a net energy balance of zero in the wild, thus allowing for daily potential positive or negative energy balance, which would translate into an increase or decrease in body mass, respectively. For purposes of this model I assumed that any excess energy intake ($> \text{DEE}$) could result in weight increases due primarily to deposition in the form of fat. I used the value of 39 kJ as the equivalent of 1 gr of fat (Ricklefs 1980). Most weight (70-90 %) gained by birds during the nonbreeding period are the result of gains in fat stores (Reinecke et al. 1982, Krapu and Johnson 1990). For simplicity, I assumed every 39 excess kJ would equal 1 gr increase in body mass and conversely a 39 kJ deficit could equal 1 gr decrease in mass, although this assumption is likely to overestimate mass gained or lost. I assumed that habitat use patterns (proportion of time spent in different habitats), obtained from aerial surveys and pooled by month, were similar for all days during a month (in essence an average day for the particular month). I assumed thermoneutrality during the entire period because the lowest temperature recorded (-2°C) during the entire study period did not surpass the Whooping Cranes' estimated lower critical temperature (-13.5°C) and it is expected that larger bird species are less

sensitive to thermal environments (Nagy 1982).

RESULTS

Monthly Energy Budgets.-- Mean DEE per month for Whooping Cranes was not significantly different ($P > 0.05$, $U = 24$, $df = 4, 7$) during the two winters of study, however gross energy intake was significantly less during the 1993-94 winter ($P = 0.01$, $U = 11$, $df = 4, 7$; Table 11). During the 1992-93 wintering season Whooping Cranes showed a consistent and high positive daily energy balance during all months (Table 11). Excess energy (based on differences between intake and expenditure) peaked in January with energy intake more than double the estimated daily expenditure during most months. During the month of March DEI was only slightly greater than DEE. During the 1993-94 wintering period comparable data on habitat use was not available for the months of November, February, and March (Chapter II, Table 11). During October and January the cranes showed a negative DEB, a positive balance in January (+126.9) and a larger increase in energy intake was estimated during the month of March (+889; Table 11).

Energetic Contribution of Food Items.-- The most significant source of energy for wintering Whooping Cranes during both years of study was blue crab. Whooping Cranes appear to rely on blue crabs for most of their daily energy intake during the winter months. Time spent in open water habitats, where blue crabs are captured, was consistently high both years during the entire wintering period (Chapter II). Use of open water habitats was particularly high during the 1992-93 season when blue crabs comprised between 62% and

98% of daily energy intake during the different months (Table 12). There were great differences in net energy obtained from blue crab between the two winters of study for the months of October, December, and January (Table 12).

During the 1992-93 winter, blue crabs contributed between 62% and 98% (mean = 88.4) of the daily energy intake during all months (Table 12). Blue crab capture rates by Whooping Cranes decreased by more than 50% from the first to second year (Chapter II, Table 5). Blue crab trapping data showed a considerable decrease in abundance of blue crabs during the second year compared to the first (Chapter II, Fig. 2). Decreased abundance of blue crabs and reduced capture rates by cranes translated into reductions in proportion of energy contributed by blue crabs to cranes' diet during most of the 1993-94 winter. Blue crab comprised between 18% and 63% (mean = 45.9%) of energy intake in October, December and January. However, in March 1994 energy intake from crabs was similar to 1992-93 values (97.6%).

Wolfberry fruit was the second most important source of energy in the overall diet of wintering Whooping Cranes along the Texas coast. The proportion of energy provided by wolfberry averaged 21.3% of DEI during the months of October through January during the winter of 1992-93; whereas during the 1993-94 winter wolfberry contributed an average 52.1% of DEI during the months of October, December and January (Table 12). Wolfberry increased significantly, relative to 1992-93, in importance in both net energy and proportion of total energy provided during the months of October, December, and January in 1993-94 winter (Table 12). The increased value of wolfberry energy was the result of increased time spent in salt marsh vegetation and greater wolfberry consumption rates during the second

Table 11. Daily energy expenditure (DEE), daily energy intake (DEI), and daily energetic balance of Whooping Cranes wintering on the Texas coast.

Month	1992-1993			1993-1994		
	GEI Kj/d kj/day	DEE kj/day	Balance kj/day	GEI kj/day	DEE kj/day	Balance kj/day
October	3186.4	2701.8	484.7	2442.4	2776.0	-333.6
November	4902.4	2556.2	2346.2			
December	5024.7	2507.6	2517.1	2322.8	2574.4	-251.62
January	7415.1	2502.4	4912.7	2620.5	2493.6	126.9
February	6678.4	2502.5	4175.9			
March	2681.6	2513.2	168.4	3133.5	2244.5	889.1
April	5055.9	2469.8	2586.0			

Table 12. Total net and proportion of daily energy obtained from different food items during different months by Whooping

Cranes wintering on the Texas coast.

Food Type	October		November		December		January		February		March		April	
	Net	%	Net	%	Net	%	Net	%	Net	%	Net	%	Net	%
1992-1993														
Blue crab	1976	62	4035	82.3	4365	86.9	7287	98	6506	97	2646	98	4694	93
Wolfberry	1154	36.2	832	17	539	10.7	0	0	0	0	0	0	0	0
Dwarf clam	43	1.3	27	0.5	18	0.4	77	1	142	2.1	19	0.7	339	7
Orthoptera	12	0.4	8	0.2	101	2	51	0.7	30	0.5	16	0.6	23	0.5
1993-1994														
Blue crab	448	18.4			1288	55.5	1675	63.9			3059	97.6		
Wolfberry	1994	81.6			960	41	873	33.3			0	0		
Razor clam	0	0			6	0.2	4	0.2			0	0		
Orthoptera	0	0			68	2.9	68	2.6			75	2.4		

year (Chapter II, Tables 2 and 5).

Based on the assumption that it takes 39 kJ to deposit one gr of fat (Karasov pers. comm.) and the fact that cranes consumed amounts of energy much greater than was required to meet their daily energy needs, cranes were capable of storing significant amounts of fat during most of the winter of 1992-93 but not during 1993-94 winter. During the 1992-93 winter Whooping Cranes could have gained a minimum of 4.3 gr of fat in a typical day in March to as high as 125.9 gr during an average day in the month of January. During 1993-94 cranes did not consume energy in quantities sufficient to store energy in form of fat until January and March. During January 1994 cranes could have stored 3.3 gr of fat during a day, while in March as much as 22.7 gr could have been stored.

DISCUSSION

Many birds species are reported to select sheltered microhabitats to reduce their overall energy expenditure (Caccamise and Weathers 1977, Shaw 1979, Stalmaster and Gessaman 1984). Whooping Cranes did not exhibit any behaviors which suggested selection to reduce exposure to wind and/or solar radiation and it appears they actually avoid areas near closed and brushy habitats (Hunt 1987). Cranes spend the entire day and all overwintering season exposed to sunlight and winds that are characteristic of coastal habitats. The lower critical temperature (predicted to be -13.5°C) was never reached during the winters of study.

In comparison to other species of birds, Whooping Cranes spend very little time

flying in the wintering grounds which is the most energetically expensive activity for birds. It is possible that because the minimum expenditure of energy Whooping Cranes may be able to spend a greater portion of the day actively searching for food apparently not concerned with any possible additional thermoregulatory costs associated with exposure to wind and sun. Winds are constant in the coastal environment where the Whooping Cranes overwinter and are likely to affect overall thermoregulatory costs (Bakken 1990). At present, however, I am unable to evaluate the overall effects that winds, and constant exposure to solar radiation, may have on the energetic balance of cranes. Because winds are continuous and consistent on a day to day basis, I assumed there were minimal differences in overall thermoregulatory costs over different days and between years of study.

Overwinter Survival and Reproductive Success.-- Winter survival is considered the major fitness component of many temperate dwelling avian species during the nonbreeding period (McNamara and Houston 1986, Rogers and Smith 1993). Because energy (fat) stores have been reported as affecting overwinter survival, the ability to store fat may be considered a measure of winter fitness (= overwinter survival) in migratory species. Overwinter survival can be expected to differ on the basis of differential quantities of fat stored during different years. During the two winters of study Whooping Cranes were capable of storing large quantities of energy reserves only during the first year (1992-93) when DEI greatly exceeded DEE during all months (Table 11). Because of the differences in potential for energy storage during the two seasons, one would expect greater survival of cranes during

the first winter relative to the second year. Actual Whooping Crane mortality recorded during the two years of study supports this prediction. Whooping Crane mortality was zero during the 1992-93 winter, while, seven Whooping Cranes were confirmed dead (and possibly up to 12 cranes may have died) during the winter of 1993-94. Reproductive success of northern latitude migratory birds may depend on the accumulation of adequate energy reserves on the wintering grounds (McLandress and Raveling 1981, Joyner et al. 1984). Fat stored during the winter may be important for reproduction upon arrival on breeding grounds for Whooping Cranes, as is suggested for several other species of northern migrants (McLandress and Raveling 1981). During many years Whooping Cranes arrive on the breeding grounds when conditions are not favorable for feeding (frozen water, lack of invertebrates and vertebrate life dormant, Brian Johns, pers. Comm.). In years when unfavorable conditions exist, securing sufficient energy reserves in wintering areas may be of critical importance for success of reproduction.

Differential nesting attempts and reproductive success between the springs of 1993 and 1994 is suggestive and appears to support the idea that energy stores from the wintering grounds may be of considerable importance for Whooping Crane reproduction during the subsequent spring. During the spring of 1993, following the winter in which Whooping Cranes had high potential to store energy reserves, a record 45 nests were located in Wood Buffalo National Park producing 36 young of which 15 arrived on the wintering grounds. In contrast, the spring of 1994, after a relatively poor food availability winter with little opportunity to store energy reserves, only 29 nesting attempts were documented producing 13 chicks of which eight arrived on the wintering grounds. Water

levels in nesting ponds are measured in the breeding grounds by the Canadian Wildlife Service and are believed to be correlated with chick production (Kuyt et al. 1992). Qualitative assessments by Canadian Wildlife Service and U.S. Fish and Wildlife Service Biologists had ranked water levels in breeding grounds during 1993 as "alarmingly low during spring and production was not expected to be very good", while in 1994 water conditions "appeared favorable" for reproduction (Stehn 1994, 1995). Based on the previous evaluations of the nesting habitat by experts, the opposite of what was expected (bad reproduction in 1993, good in 1994) was observed (good reproduction in 1993, bad in 1994) regarding nesting attempts and nesting success.

Whooping Cranes could secure energy reserves at stopover areas while in route to breeding grounds during spring as several other species appear to do. Sandhill Cranes, for example, spend significant amounts of time (several days to weeks) in stopover areas during spring migration (Krapu et al. 1985,). Because of the extended period of time spent by Sandhill Cranes in staging areas they can take on significant amount of energy during this migration period where they have been reported to gain weight at a rate as high as 25 g.d^{-1} (Krapu et al. 1985). Whooping Cranes generally do not spend extended periods of time at any location during spring migration and, therefore are not likely to consume enough food during migration to store significant amounts of energy.

In addition to increased overwinter mortality in 1993-94 winter and bad reproductive success in 1994, several other aspects of Whooping Cranes' wintering ecology suggest the winter of 1993-94 was a bad year to procure resources. The proportion of cranes detected in relation to total number of cranes known wintering in area was

significantly different during the two winters (Chapter II). In 1992-93, 96.7% of the wintering crane population was detected in aerial surveys, while during 1993-94 the proportion of cranes detected in surveys declined to 89.4%. Because the same area was surveyed each year with the same route and observers this difference suggests that Whooping Cranes may have moved away from their normal wintering range in the salt marshes in search of resources.

Two aspects of migration were different during the spring and summer of 1994, late migration and oversummering cranes. Whooping Cranes begin migrating later than usual in 1994 with 15 cranes remaining in ANWR and MINWR until early May which is an unprecedented event (Stehn 1994). In addition, three Whooping Cranes in 1994 spent the spring and summer at ANWR. Oversummering cranes have been reported on a few occasions over that last 50 years. The phenomena of oversummering is not unusual in other groups of birds and has been reported in at least 15 families (McNeil et al. 1994). In shorebirds, which are the most common oversummering species, the primary reason reported to cause oversummering is the absence or delayed physiological changes prior to spring migration which include molting and accumulation of large amounts of fat (Johnson et al. 1989, McNeil 1994). The delayed initiation of migration by large numbers of cranes and the presence of the largest numbers of oversummering Whooping Cranes during spring and summer may be an indication of the limited opportunity for energy storage during the 1993-94 winter period.

Population Energetics.-- Based on the results of 1992-93 winter, the average DEE throughout the winter is $2536.2 \text{ kJ} \cdot \text{d}^{-1}$. An average 88% of the energy consumed was obtained from blue crabs during the winter period, therefore 2231 kJ was attributed to blue crabs. I assumed that in a normal year individual crabs in the population average 110 gr of which cranes consume 90% of it. A single crane could meet its average daily energy needs (actually 88% mean contribution by blue crab) by consuming 5.26 crabs, weighing 110 gr, during its daily foraging. A population of 130 Whooping Cranes would require 290,141 assimilable kJ for a single day during the winter. The 130 cranes would require 817,299 gr of ingested blue crab, which is equal to 683.8 crabs, to meet DEE during a single day during the wintering period.

Winter food shortages in wintering grounds may naturally influence overwinter survival and reproductive success during the breeding season in Whooping Cranes. Blue crab has been consistently cited as an important food source for Whooping Cranes during the winter by researchers and workers at Aransas National Wildlife Refuge. Based on energy obtained from blue crab supports previous reports, and further highlights, that crab may be a very important and at times a critical source of food and energy for Whooping Cranes wintering in Texas. Whooping Cranes consumed energy far in excess of DEE during 1992-93 winter suggesting the cranes were attempting to store energy reserves throughout the wintering period. Because of the decreased abundance of blue crab during 1993-94 winter Whooping Cranes were not capable of securing sufficient resources to store significant amount of energy which may have lead to increased overwinter mortality and decreased reproductive effort and output.

CHAPTER V

SUMMARY AND CONCLUSIONS

My data on macrohabitat use show that Whooping Cranes spend most of their time during the winter in the salt marsh areas of the coast with upland and bay areas used only to a small extent. During the two winters of study 87% and 86% of all crane recorded on aerial surveys were found in salt marsh habitats, while 8.8% and 11% were found in uplands, and only 3.9% and 3.1% were located in bays. The salt marsh is, therefore, the most important habitat for Whooping Cranes' daily activities. The use of upland and bays appears to be opportunistic and in response to readily available food supplies. For example, the use of uplands is associated with areas that have been recently burned (Chavez-Ramirez et al. 1996), and cranes have only rarely been observed in upland areas that have not been recently burned. The only period of intensive use of bay areas by cranes, during the study period, was during a two week period in March 1993 that corresponded to a sudden increase in abundance of dwarf clams. The opportunistic use of uplands and bays may be a trait that can be incorporated into future management programs. For example, it is clear that the cranes are capable of locating unusual sources of abundant food resources.

The results of my study are in agreement with previous reports regarding the importance of blue crab and wolfberry in the winter diet of Whooping Cranes. My results show wolfberry contributes an important proportion of the overall energy consumed during the early portion of the overwintering period, October through January, and ceases to be

important in the latter part of the wintering season, February through April, when fruit ripening ceases. Blue crabs, however, appear to be the most important source of food and energy for wintering Whooping Cranes contributing between 62% and 97% of overall energetic intake during different months. My results show, however, that blue crabs may become a limited resource during some years. The decreased abundance and availability of blue crab during the 1993-94 winter resulted in decreased overall energy intake, with blue crabs contributing as little as 18.4% of total energetic intake during the early part of the winter. The decreased energetic intake due to the decrease in the blue crab numbers was only partially offset by increased consumption of wolfberry fruit. Even with increased wolfberry intake, the lack of crabs affected the potential for energy storage throughout the wintering period resulting in negative energy balances through the first half of the 1993-94 winter.

Several aspects of the Whooping Cranes' winter ecology reflect possible effects of reduced energetic intake rates. Greater than normal overwinter mortality during the 1993-94 winter may be related to the negative energy balance. Further evidence of the negative effects of decreased energetic intake is the unprecedented, delayed initiation of spring migration by a large number of cranes resulting in the presence of Whooping Cranes through the month of May at ANWR. The presence and oversummering of at least three cranes in ANWR and MINWR are further indications of the possibility of reduced crab availability affecting energy reserves necessary for migrating.

The possibility exists that energetic reserves obtained from the wintering grounds are important for spring reproductive efforts, as they are in other migratory species, making

the availability of sufficient food and energy resources in the wintering grounds of greater significance in the overall well-being of this population. The possibility that food resources in the wintering grounds contribute to reproductive efforts and success in the breeding grounds had not been previously considered for Whooping Cranes. Future work should be attempted in trying to evaluate the significance of resource availability on the wintering grounds in relation to overwinter survival and in the overall fitness (reproductive success, lifespan etc.) of Whooping Cranes.

Careful monitoring of blue crab numbers in the salt marshes of the Whooping Cranes wintering range should be undertaken on a yearly basis and regularly throughout the wintering season. Careful monitoring of crabs may help in predicting periods of food shortage for the cranes on the wintering grounds which may help in determining whether management alternatives need to be implemented. For example, during a year of low crab availability it will be more important to implement regular burns through out the winter, and perhaps increase the number of burns, in an effort to provide alternative sources of food and energy for the cranes.

The extremely low abundance of blue crabs during the 1993-94 winter was due to mortality associated with an extreme low tide that occurred during August and September 1993. The effect of this low tide was that water levels decreased below the substrate of the marshes and all marine life perished. Blue crabs were observed to begin to move back into the marsh in January of 1994, although most were less than 25 cm in length and were not captured in my traps. Commercial crab trappers were identified as a potential problem that may affect the rate of movement of crabs to the marshes, and feeding areas of cranes. The

traps, numbering in the hundreds, are set along the bay areas adjacent to Whooping Crane salt marsh areas. Traps set in close proximity to the marsh may intercept the bigger crabs which are attempting to move into the marsh. Consideration should be given to the development of a mechanism by which crab trapping may be regulated, particularly during years of low crab numbers. Some specific measures that may be implemented could include the establishment of a minimum distance from the salt marsh at which traps may be set. Elimination of crab trapping, or implementing a minimum distance for setting traps, may facilitate and increase the rate at which blue crabs will move to the shallow areas and become available for cranes.

We now have information regarding the importance of blue crab abundance and know of the possibility that crabs may become limiting during some years. Information presented here provides data on numbers of crabs necessary to maintain a single crane and a population of 130 cranes over a day. This information may be used to extrapolate food requirements over the entire season or portions of it. What remains to be determined is what the actual density of crabs is at different locations and at times of the year during high and low crab abundance years. Changes in crab population levels throughout the annual cycle are of great importance in that knowledge of crab densities can help us evaluate several aspects of the Whooping Cranes' winter ecology. With information on crab densities minimum territory size can be determined for a pair and/or family group during different years. Territory size is important as the average territory size on the wintering grounds has been decreasing over time (Stehn and Johnson 1987). Minimum territory size may also help in determining the carrying capacity of the current wintering grounds on and

around Aransas and may help in predicting maximum number of cranes which may be supported. Being able to determine carrying capacity may also help in the evaluation of future potential wintering grounds for the planned reintroduced populations of Whooping Cranes.

LITERATURE CITED

- Alatalo, R. V. 1980. Seasonal dynamics of resource partitioning among foliage-gleaning passerines in northern Finland. *Oecologia* 45:190-196.
- Allen, R. P. 1952. The whooping crane. National Audubon Society Research Report No. 3.
- Alonso, J. A., and J. C. Alonso. 1993. Age related differences in time activity budgets and parental care in wintering Common Cranes. *Auk* 110:78-88.
- Alonso, J. A., J. C. Alonso, L. M. Carrascal, and R. Munoz-Pulido. 1994. Flock size and foraging decisions in central place foraging White Storks, *Ciconia ciconia*. *Behaviour* 129:279-292.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.
- Amat, J. A., and F. D. Rilla. 1994. Foraging behavior of White-faced Ibises (*Plegadis chihi*) in relation to habitat, group size, and sex. *Colon. Waterbirds* 17:42-49.
- Ankney, C. D., and R. T. Alisauskas. 1991. The use of nutrient reserves by breeding waterfowl. Proc. 20th Inter. Ornith. Congress, Christchurch, New Zealand. Vol. I:21070-2176.
- Aschoff, J., and H. Pohl. 1970. Rhythmic variations in energy metabolism. *Fed. Proc.* 2:1541-1552.
- Audubon, J. J. 1841. *The birds of America*. Macmillan, New York.

- Bakken, G. S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. *Auk* 107:587-594.
- Bamford, O. S., and G. M. O. Maloiy. 1980. Energy metabolism and heart rate during treadmill exercise in the Marabou stork. *J. Appl. Physiol.* 49:491-496.
- Bent, A. C. 1926. Life histories of North American marsh birds. U.S. Nat. Mus. Bull. no. 135.
- Bishop, M. A., and D. R. Blankinship. 1982. Dynamics of subadult flocks of whooping cranes at Aransas National Wildlife Refuge, Texas, 1981. Pages 180-189 in Proc. 1981 Crane Workshop (J.C. Lewis, Ed.). National Audubon Society, Tavernier, Florida.
- Bishop, M. A. 1984. The dynamics of subadult flocks of whooping cranes wintering in Texas, 1978-79 through 1982-83. Unpubl. MS thesis, Texas A&M Univ., College Station.
- Blankinship, D. R. 1976. Studies of whooping cranes on the wintering grounds. Pages 197-206 in Proc. Int. Crane Workshop (J.C. Lewis, Ed.). Oklahoma State Univ. Publ. and Print., Stillwater.
- Blem, C. R. 1990. Avian energy storage. *Curr. Ornithol.* 7:59-113.
- Britton, J. C., and B. Morton. 1989. Shore ecology of the Gulf of Mexico. Univ. of Texas Press, Austin.
- Brown, J. L. 1964. Territorial behavior and population regulation of birds. *Wilson Bull.* 81:293-329.
- Butler, R. W. 1994. Population regulation of wading ciconiiform birds. *Colon. Waterbirds*

17:189-199.

- Buttemer, W. A., A. M. Hayworth, W. W. Weathers, and K. A. Nagy. 1986. Time-budget estimates of avian energy expenditure: physiological and meteorological considerations. *Physiol. Zool.* 59:131-149.
- Caccamise, D. F., and W. W. Weathers. 1977. Winter nest microclimate of monk parakeets. *Wilson Bull.* 89:346-349.
- Calder, W. A., and J. R. King. 1974. Thermal and caloric relations of birds. Pages 259-413 in *Avian biology* (D.S. Farner and J.R. King, Eds.). Academic Press, New York.
- Caraco, T. 1980. Avian flocking in the presence of a predator. *Nature* 285:400-401.
- Carrascal, L. M., L. M. Bautista, and E. Lazaro. 1993. Geographical variation in density of white stork, *Ciconia ciconia*, in Spain: Influence of habitat structure and climate. *Biol. Conserv.* 65:83-87.
- Chavez-Ramirez, F., H. E. Hunt, R. D. Slack, and T. V. Stehn. 1996. Ecological correlates of Whooping Crane use of fire-treated upland habitat. *Conserv. Biol.* 10:217-223.
- Crook, J.H. 1965. The adaptive significance of avian social organizations. *Symp. Zool. Soc. Lond.* 14:181-218.
- Davies, J. C., and F. Cooke. 1983. Annual nesting productivity in snow geese: prairie droughts and arctic springs. *J. Wildl. Manage.* 47:291-296.
- Fasola, M. 1994. Opportunistic use of foraging resources by heron communities in southern Europe. *Ecography* 17:113-123.
- Ford, H. A., L. Huddy, and H. Bell. 1990. Seasonal changes in foraging behavior of three

passerines in Australian eucalyptus woodland. Pages 245-253 in Avian foraging: theory, methodology, and applications (M.L. Morrison, C.J. Ralph, J. Verner, and J.R. Jehl, Jr, Eds.). SAB No. 13.

Goldstein, D. L. 1988. Estimates of daily energy expenditure in birds: the time energy budget as integrator of laboratory and field studies. *Am. Zool.* 28:829-844.

Goldstein, D. L. 1990. Energetics of activity and free living in birds. Pages 423-426 in Avian foraging: theory, methodology, and applications (M.L. Morrison, C.J. Ralph, J. Verner, and J.R. Jehl, Jr, Eds.). SAB No. 13.

Goss, N. S. 1886. A revised catalogue of the birds of Kansas. Kansas Publ. House, Topeka.

Goss-Custard, J. D. 1985. Foraging behavior of wading birds and the carrying capacity of estuaries. Pages 169-188 in Behavioral ecology: ecological consequences of adaptive behavior (R.M. Sibly and R.H. Smith, Eds.). Blackwell, Oxford, UK.

Hejl, S. L., and J. Verner. 1990. Within-season and yearly variation in avian foraging locations. Pages 202-209 in Avian foraging: theory, methodology, and applications (M.L. Morrison, C.J. Ralph, J. Verner, and J.R. Jehl, Jr, Eds.). SAB No. 13.

Hejl, S. L., J. Verner, and G. W. Bell. 1990. Sequential versus initial observations in studies of avian foraging. Pages 166-173 in Avian foraging: theory, methodology, and applications (M.L. Morrison, C.J. Ralph, J. Verner, and J.R. Jehl, Jr, Eds.). SAB No. 13.

Holland, A. F., and J. M. Dean. 1977. The biology of the stout razor clam Tagelus plebius: II. Some aspects of the population dynamics. *Chesapeake Science* 18:188-196.

- Holmes, R. T. 1966. Feeding ecology of the red-backed sandpiper (Calidris alpina) in arctic Alaska. *Ecology* 47:32-45.
- Hunt, H. E. 1987. The effects of burning and grazing on habitat use by whooping cranes and sandhill cranes on the Aransas National Wildlife Refuge, Texas. Unpubl. PhD dissertation, Texas A&M Univ., College Station.
- Hunt, H. E., and R. D. Slack. 1987. Winter foods of the Whooping Crane based on stomach content analyses. Pages 217-218, in Proceedings of the 1985 Crane Workshop (J.C. Lewis, Ed.). Platte River Whooping Cranes Habitat Maintenance Trust, Grand Island, Nebraska.
- Hunt, H. E., and R. D. Slack. 1989. Winter diets of whooping and sandhill cranes in south Texas. *J. Wildl. Manage.* 53:1150-1154.
- Hutto, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pages 455-476 in Habitat selection in birds (M.L. Cody, Ed.). Academic Press, New York.
- Illius, A. W., and C. Fitzgibbon. 1994. Costs of vigilance in foraging ungulates. *Anim. Behav.* 47:481-484.
- Johnsgard, P. A. 1983. *Cranes of the world*. Croom Helm, London, UK.
- Johnson, O. W., M. L. Morton, P. L. Bruner, and P. M. Johnson. 1989. Fat cyclicality, predicted migratory fat ranges, and features of wintering behavior in Pacific Golden Plovers. *Condor* 91:156-177.
- Joyner, D. E., R. D. Arthur, and B. N. Nelson. 1984. Winter weight dynamics, grain consumption and reproductive potential in Canada Geese. *Condor* 86:275-280.

- Karasov, W. H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. Pages 391-415 in Avian foraging: theory, methodology, and applications (M.L. Morrison, C.J. Ralph, J. Verner, and J.R. Jehl, Jr, Eds.). SAB No. 13.
- Kendeigh, S. C., V. R. Dol'nik, and V. M. Gavrilov. 1977. Avian energetics. Pages 127-204 in Granivorous birds in ecosystems: their evolution, populations, energetics, adaptations, impact and control (J. Pinowski and S.C. Kendeigh, Eds.). IBP 12. Cambridge Univ. Press, Cambridge, UK.
- Kennedy, M., and R. D. Gray. 1994. Agonistic interactions and the distribution of foraging organisms: Individual costs and social information. *Ethology* 96:155-165.
- King, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pages 4-70 in Avian energetics (R.A. Paynter, Ed). Publ. Nuttall Ornithol. Club No. 15, Cambridge, Massachusetts.
- Krapu, G. L., G. C. Iverson, K. J. Reinecke, and C. M. Boise. 1985. Fat deposition and usage by arctic-nesting Sandhill Cranes during spring. *Auk* 102:362-368.
- Krapu, G. L., and D. H. Johnson. 1990. Conditioning of sandhill cranes during fall migration. *J. Wildl. Manage.* 54:234-238.
- Kushlan, J. A. 1976. Feeding ecology of wading birds. Pages 249-297, in Wading Birds (A.S. Sprunt, J.C. Ogden, and S. Winckler, Eds.). National Audubon Society Research Report No. 7. New York.
- Kushlan, J. A. 1981. Resource use strategies of wading birds. *Wilson Bull.* 93:146-163.

- Kuyt, E., S. J. Barry, and B. W. Johns. 1992. Below average whooping crane production in Wood Buffalo National Park during drought years 1990 and 1991. *Blue Jay* 50:225-229.
- Labuda, S. E., and K. O. Butts. 1978. Habitat use by wintering whooping cranes on the Aransas National Wildlife Refuge. Pages 151-157 in *Proceedings 1978 Crane Workshop* (J.C. Lewis, Ed.). Colorado State Univ. Print. Serv., Fort Collins.
- Lack, D. 1966. *Population studies of birds*. Claredon Press, Oxford, UK.
- Lawrence, E. S. 1985. Vigilance during easy and difficult foraging tasks. *Anim. Behav.* 33:1373-1375.
- Lehikoinen, E. 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. *Ornis Scandinavica* 18:216-226.
- Lendrem, D. W. 1983. Predation risk and vigilance in the blue tit (*Parus caeruleus*). *Behav. Ecol. Sociobiol.* 14:9-13.
- Lima, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the blackcapped chickadee. *Oecologia* 66:60-67.
- Lima, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *Wilson Bull.* 105:1-47.
- Lundquist, R. W., and D. A. Manuwal. 1990. Seasonal differences in foraging habitat of cavity-nesting birds in the southern Washington Cascades. Pages 218-225 in *Avian foraging: theory, methodology, and applications* (M.L. Morrison, C.J. Ralph, J. Verner, and J.R. Jehl, Jr, Eds.). SAB No. 13.

- Mabie, D. W., L. A. Johnson, B. C. Thompson, J. C. Barron, and R. B. Taylor. 1989. Responses of wintering whooping cranes to airboat and hunting activities on the Texas coast. *Wildl. Soc. Bull.* 17:249-253.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599-619.
- MacArthur, R. H. 1972. *Geographical Ecology*. Harper and Row, New York.
- MacNeil, R., M. T. Diaz, and A. Villeneuve. 1994. The mystery of shorebird over-summering: a new hypothesis. *Ardea* 82:143-152.
- Martella, M. B., D. Renison, and J. L. Navarro. 1995. Vigilance in the Greater Rhea: effects of vegetation height and group size. *J. Field Ornithol.* 66:215-220.
- Martin, T. E. 1986. Competition in breeding birds: on the importance of considering processes at the level of the individual. *Curr. Ornithol.* 4:181-210.
- Mayhew, P., and D. Houston. 1989. Feeding site selection by Widgeon (*Anas penelope*) in relation to water. *Ibis* 131:1-8.
- McLandress, M. R., and D. G. Raveling. 1981. Changes in diet composition of Canada geese before spring migration. *Auk* 98:65-79.
- McNamara, J. M., and A. I. Houston. 1986. The common currency of behavioral decisions. *Am. Natur.* 127:358-378.
- Metcalf, N. B. 1984. The effects of habitat on vigilance of shorebirds: is visibility important? *Anim. Behav.* 32:981-985.
- Metcalf, N. B., and R. W. Furness. 1984. Changing priorities: the effect of pre-migratory

- fattening on the trade-off between foraging and vigilance. *Behav. Ecol. Sociobiol.* 15:203-206.
- Miles, D. B. 1990. The importance and consequences of temporal variation in avian foraging behavior. Pages 210-217 in *Avian foraging: theory, methodology, and applications* (M.L. Morrison, C.J. Ralph, J. Verner, and J.R. Jehl, Jr, Eds.). SAB No. 13.
- Montagna, P. A., and R. D. Kalke. 1992. The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces estuaries, Texas. *Estuaries* 15:307-326.
- Moreira, F. 1994. Diet, prey-size selection, and intake rates of Black-tailed Godwits, Limosa limosa, feeding on mudflats. *Ibis* 136:349-355.
- Moreno, J., and L. Hillstrom. 1992. Variation in time and energy budgets of breeding wheatears. *Behaviour* 120:11-39.
- Morrison, M. L., and K. A. With. 1987. Intersexual and interseasonal resource partitioning in Hairy and White-headed Woodpeckers. *Auk* 104:225-233.
- Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. *Wildlife-habitat relationships, concepts and applications*. Univ. of Wisconsin Press, Madison.
- Morse, D. H. 1990. Food exploitation in birds: some current problems and future goals. Pages 134-143 in *Avian foraging: theory, methodology, and applications* (M.L. Morrison, C.J. Ralph, J. Verner, and J.R. Jehl, Jr, Eds.). SAB No. 13.
- Nagy, K. A. 1989. Field bioenergetics: accuracy of models and methods. *Physiol. Zool.* 62:237-252.

- Nelson, J. T. 1995. Nutritional quality and digestibility of foods eaten by Whooping Cranes on their Texas wintering grounds. Unpubl. MS thesis, Texas A&M Univ., College Station.
- Netting, M. G. 1927. Amphibians and reptiles in relation to birds. *Cardinal* 2:2-28.
- Nuttall, T. 1834. A manual of ornithology of the United States and Canada. Water Birds. Hillard and Brown, Boston, Massachusetts.
- Pianka, E. R. 1994. *Evolutionary Ecology*. Harper Collins College Publishers, New York.
- Pienkowski, M. W., P. N. Ferns, N. C. Davidson, and D. H. Worrall. 1984. Balancing the budget: measuring the energy intake and requirements of shorebird in the field. in Coastal waders and wildfowl in winter (P.R. Evans, J.D. Goss-Custard, and W.G. Hale, Eds.). Cambridge Univ. Press, Cambridge, UK.
- Pöysä, H. 1987. Feeding-vigilance trade-off in the teal (Anas crecca): effects of feeding method and predation risk. *Behaviour* 103:108-122.
- Pulliam, H. R., and T. Caraco. 1984. Living in groups: Is there an optimal group size. Pages 122-147 in Behavioral ecology: an evolutionary approach (J.R. Krebs and N.B. Davies, Eds.). 2nd edition. Blackwell, Oxford, UK.
- Reinecke, K. J., T. L. Stone, and R. B. Owen. 1982. Seasonal carcass composition and energy balance of female black ducks in Maine. *Condor* 84:420-426.
- Ricklefs, R. E. 1980. *Ecology*. Chiron Press, New York.
- Rogers, C. M., and J. N. M. Smith. 1993. Life-history theory in the nonbreeding period: trade-offs in avian fat reserves? *Ecology* 74:419-426.

- Schluter, D. 1982. Seed and patch selection by Galapagos ground finches: relation to foraging efficiency and food supply. *Ecology* 63:1504-1517.
- Sealy, S. G. 1979. Extralimital nesting of Bay-breasted Warblers: response to forest tent caterpillars? *Auk* 96:600-603.
- Shaw, G. 1979. Functions of dipper roosts. *Bird Study* 26:171-178.
- Shields, R. H., and E. L. Benham. 1969. Farm crops as supplements for whooping cranes. *J. Wildl. Manage.* 33:811-817.
- Smith, J. N. M., P. R. Grant, B. R. Grant, I. J. Abbott, and L. K. Abbott. 1978. Seasonal variation in feeding habits of Darwin's ground finches. *Ecology* 59:1137-1150.
- Stalmaster, M. V., and J. A. Gessaman. 1984. Ecological energetics and foraging behavior of overwintering bald eagles. *Ecol. Monogr.* 54:407-428.
- Stehn, T. V. and F. E. Johnson. 1987. Distribution and winter territories of Whooping cranes on the Texas coast. Pages 180-195, in *Proceedings of the 1985 Crane Workshop* (J.C. Lewis, Ed.). Platte River Whooping Cranes Habitat Maintenance Trust, Grand Island, Nebraska.
- Stehn, T. V. 1994. Whooping Cranes during the 1994 winter. Aransas National Wildlife Refuge files, Austwell, Texas.
- Stehn, T. V. 1995. Whooping Cranes during the 1995 winter. Aransas National Wildlife Refuge files, Austwell, Texas.
- Stevenson, J. O., and R. E. Griffith. 1946. Winter life of the whooping crane. *Condor* 48:160-178.

- Swengel, S. 1992. Sexual size dimorphism and size indices of six species of captive cranes at the International Crane Foundation. *Proc. North Am. Crane Workshop* 6:151-158.
- Uhler, F. M., and L. N. Locke. 1969. A note on the stomach contents of two Whooping Cranes. *Condor* 52:216.
- Ulfstrand, S. 1976. Feeding niches of some passerine birds in a south Swedish coniferous plantation in winter and summer. *Ornis Scandinavica* 7:21-27.
- USFWS. 1986. Whooping Crane recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.
- Walsberg, G. E. 1983. Avian ecological energetics. Pages 161-220. *in* *Avian Biology* (D.S. Farner, J.R. King, and K.C. Parkes, Eds.). Vol. VII. Academic Press, New York.
- Weathers, W. W., and K. A. Sullivan. 1993. Seasonal patterns of time and energy allocation by birds. *Physiol. Zool.* 66:511-563.
- Wiens, J.A. 1989. *The ecology of bird communities: vol 2, processes and variations.* Cambridge Univ. Press, Cambridge, UK.
- Wiens, J. A., and J. T. Rotenberry. 1990. Diet niche relationships among North American grassland and shrubsteppe birds. *Oecologia* 42:253-292.
- Williams, J. E., and S. C. Kendeigh. 1982. Energetics of the Canada goose. *J. Wildl. Manage.* 46:588-600.

VITA

Felipe Chavez-Ramirez was born on 26 May, 1965 to Felipe and Martina Chavez in Chihuahua City, Chihuahua, Mexico. He attended grades 1-2 at Kermit Primary School, Kermit TX; grades 3-4 at Wink Elementary, Wink, TX; grade 5 at Fray Pedro De Gante, Chihuahua City, Chih.; grade 6 at Praxedis G. Guerrero, Chihuahua City, Chih.; grades 7-9 at Escuela Secundaria Estatal No. 9, Chihuahua, City, Chih.; Grades 10-12 at Escuela Tecnica Forestal No. 3, Saltillo, Coahuila. He graduated as a Forestry Technician in 1984.

From July 1984 to January 1985 Felipe worked for the Subdelegacion de Ecologia, SEDUE in Chihuahua. From February to June 1985 he worked for the Servicio Forestal (forest service) in the state of Chihuahua. Felipe enrolled in college in the summer of 1985 and ultimately received a B.S. in Biology from Sul Ross State University, Alpine, TX in December 1988.

In January 1989, Felipe began graduate studies at Texas A&M University, and was awarded his M.S. in Wildlife and Fisheries Sciences in May 1992. For his master's thesis Felipe studied the effect of birds and mammals in the dispersal of Ashe Juniper seeds under the direction of Dr. R. Douglas Slack.

Felipe remained at Texas A&M University after completing his masters to pursue a Ph.D. investigating food availability, foraging ecology and energetics of whooping cranes wintering in Texas. Felipe's permanent address is Degollado # 3504, Chihuahua, Chih., 31400, Mexico.